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RECENT ADVANCES IN THE STUDY OF HEREDITY

(A Course of Lectures, for the University of London, delivered in the Summer Term, 1909).

BY A. D. DARBISHIRE.

LECTURE VII.

CYTOLOGICAL AND OTHER EVIDENCE RELATING TO THE INHERITANCE OF SEX.

BEFORE passing to the main subject of this Lecture, *i.e.*, to a consideration of those phenomena which point to the *male* as being heterozygous for sex, reference may be made to certain theories of sex-inheritance in man. Theories have been held, and suggestions made, on the cause of sex since the time of Hippocrates, who thought that males resulted from the mixing of the products of the right generative glands of the male and female, and females from the products of the left. This theory was revived by Hencke in 1786 and has been brought forward again recently, in a modified form, by Dr. Rumley Dawson.[1] According to Dr. Dawson the female determines the sex of a child: the right ovary gives rise only to potentially male ova, the left to female ova. The evidence advanced in support of this view is very unsatisfactory: for the data of greatest value bearing upon this hypothesis, *viz.*, the sex of children borne by a female on whom unilateral ovariotomy has been performed, is rendered worthless from the acknowledged impossibility of being certain whether the whole ovary had been removed, and by the known fact that fragments of an ovary may liberate ova capable of fertilisation and development. Dr. Dawson's book is, however, interesting, because the conclusions reached in it that the female bears two kinds of eggs, ♂-producing and ♀-producing, whilst the male plays no part in determining sex, is strikingly similar to that arrived at by Mendelian analysis.

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[1] G. Rumley Dawson. The Causation of Sex. London, 1909. [H. K. Lewis].

Observations on the reproductive bodies of organisms, spores and gametes, indicate that although the asexual spores of all the higher plants have been shown to be differentiated into two kinds, destined to produce male or female gametes; yet up to the present only a few organisms, and these animals, have been shown to possess morphologically differentiated gametes pre-destined with regard to sex. I refer to (1) *Hydatina*, *Dinophilus* and *Phylloxera*, which have two kinds of ova, large and small, the former destined to become female zygotes, the latter male: (2) to *Paludina*, and other molluscs, and possibly some Protozoa, which have dimorphic sperms, differing in size, shape and sometimes in the number of cilia they bear.

Observations on the cytological characters of gametes, however, have disclosed in a large number of cases, striking phenomena pointing to complete sex differentiation of the gametes. It has been found in a large number of Arthropods (chiefly Insecta, Myriapoda and Arachnida) and a few other animals, that one half of the sperms differ from the other half in chromosome characters. In 1891 Henking discovered that the sperms of *Pyrrochoris*, a hemipteran genus, are dimorphic in chromosome characters, half the sperms having one chromosome more than the others. MacClung suggested in 1902 that probably this differentiation was correlated with sex-determination, but it was left to Wilson and Stevens to describe the phenomena more exactly and extend the observations to Orthoptera and other Arthropoda. A large number of species possessing such dimorphic sperms have now been recorded by Wilson and his fellow workers. In all these cases it may be said that half the sperms possess something more than the other half, *i.e.*, one or more additional chromosomes; this additional body has been called the *x-element*, *accessory chromosome*, or *idiochromosome*. If several chromosomes constitute the x-element, they are found to behave as one chromosome in the cell-divisons. The remaining sperms may only differ from the former class of sperms in the absence of the x-element, or they may have in addition a *y-element* in place of the x-element, *i.e.*, one or more peculiar chromosomes which differ from all the other chromosomes. Thus a species may possess one of the two sets of sperms, which have the following chromosome formula :—

$$\text{(a)}\quad \tfrac{1}{2}(c + x) \quad \tfrac{1}{2}c$$
$$\text{or (b)}\quad \tfrac{1}{2}(c + x) \quad \tfrac{1}{2}(c + y)$$

where $c =$ the number of chromosomes common to both kinds of sperms, $y = 1$ peculiar chromosome, $x = 1$ to 4 peculiar chromosomes. It may be noted here that the x- and y-elements are "synaptic mates," as indicated in the spindle in Fig. 4.

A remarkable fact has now to be related. In species presenting dimorphic sperms as just described, it is found that the somatic cells of the male and female are different in their chromosome characters! The female somatic cells have $(2c + 2x)$ chromosomes, where $c =$ equals the number of chromosomes common to the two kinds of sperms, and $x =$ the x-element again ; but the male somatic cells contain either $(2c + 1x)$ or $(2c + x + y)$ chromosomes according to whether half the sperms have a y-element or not. Now it has been found that the ova eliminate

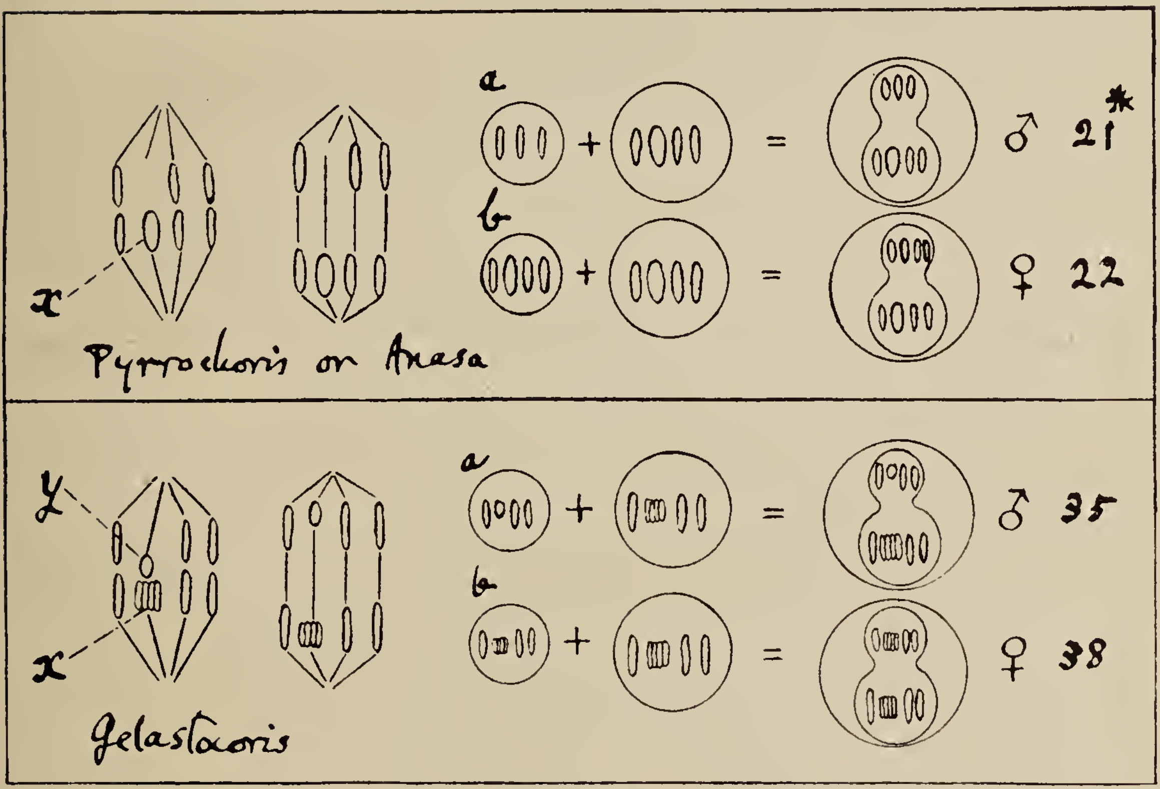

Fig. 4.

Fig. 4. Diagram of cytological phenomena manifested in gametogenesis and in the soma of certain insects (after Wilson[1]).

$x =$ x-element or accessory chromosome.
$y =$ y-element, $a =$ male-producing sperm.
$b =$ female-producing sperm.

* These numbers refer to *Anasa* only.

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[1] Recent Researches on the Determination and Heredity of Sex. Science, N.S., Vol. 29, No. 732, pp. 53-70.

one x-chromosome in the reducing division; hence the mature ovum contains $c + x$ chromosomes, for the germ and somatic cells are alike in chromosome characters. It is therefore a just inference that the following combinations have occurred:—

Sperms.	Ova.	Zygote.	Sex.
c or $(c + y)$	$+ (c + x)$	$= (2c + x)$ or $(2c + x + y)$	♂
$(c + y)$	$+ (c + x)$	$= (2c + 2x)$	♀

(cf. Diagram in Fig 4).

Hence it follows that the sperms carrying the x-element are female-producing, whilst the sperms without the x-element or with the y-element are male-producing.

Thus we see that in all these cases the male gives rise to two kinds of sperms, ♂-producing or ♀-producing, while the female produces ova all alike and apparently all ♀-producing, as will be shown more clearly in the parthenogenetic cases shortly to be described. It is evident therefore that the male can be compared exactly to a Mendelian heterozygote (DR), which is heterozygous for maleness and femaleness (♂ ♀) with maleness dominant, and the female to a recessive (RR) homozygous for femaleness (♀ ♀).

Consequently a Mendelian interpretation of sex would seem to be fully established in a large number of cases. Moreover, since a long series of species can be arranged leading from forms like *Pyrrochoris* or *Anasa*, which have a simple x-element and no y-element, to forms like *Nezara*, which have x- and y-elements almost indistinguishable, Wilson has suggested that possibly all the sperms, at least in allied animals, may be differentiated with regard to sex-potentialities, although cytologically they are all alike. This theory of sex is supported in a remarkable manner by the phenomena exhibited by the chromosomes in the maturation of ova, and in the spermatogenesis in animals such as Ants, Bees, Hornets, the green flies (Aphids) and the vine pest, *Phylloxera*, which reproduce both sexually and asexually (*i.e.*, parthenogetically).

It is well-known that drone (*i.e.*, ♂) bees are produced parthenogenetically by the females, and that females, whether workers or queens, are produced only from fertilised eggs. The females of Aphids and *Phylloxera*, however, produce both males and females parthenogenetically, but here again fertilised eggs always develop into females. These facts, naturally enough, were urged against the views we have just discussed. But when the cytological phenomena in gametogenesis had been worked out, the apparently contradictory facts were ultimately brought into line. Indeed it happens not rarely that facts apparently inimical to a theory become later the strongest supports of that theory if they become harmonised with it.

The parthenogenetic ova in Aphids and *Phylloxera* do not undergo reduction in maturation and it is found that the ova destined to become males contain one chromosome less than the female ova, the odd chromosome probably being extruded with a mass of protoplasm in a pseudo-heterotype division (see Fig. 5). Hence all the cells of the females have one more chromosome than the cells of the males, which have five chromosomes.

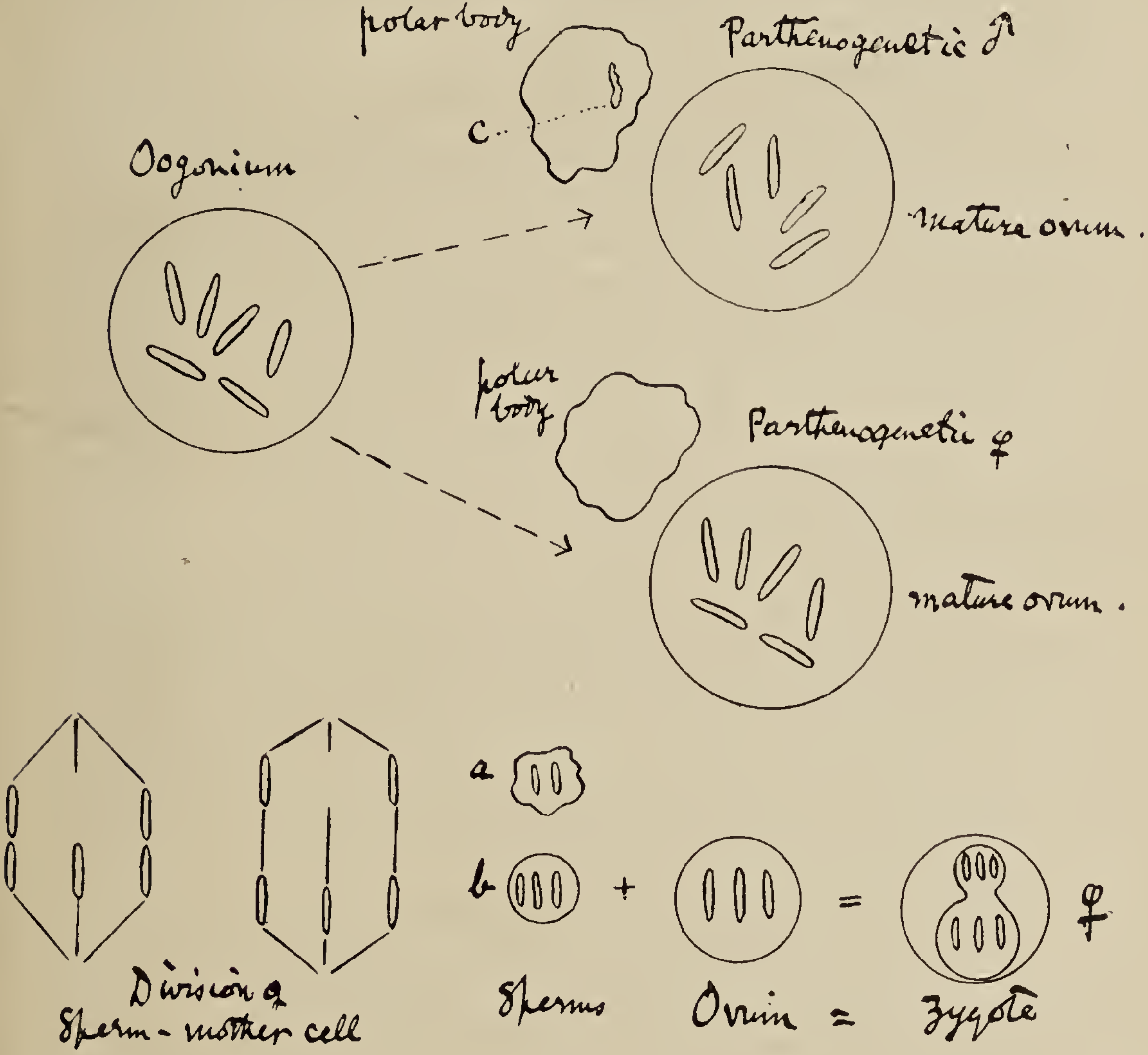

Fig. 5.

Fig. 5. Diagram of cytological phenomena manifested in the formation of the parthenogenetic ova and gametes in Aphids. *a*, Sterile spermatozoa. *b*, Fertile spermatozoa. *c*, Chromosome, probably extruded in polar body.

The extra chromosome of the female is therefore undoubtedly the equivalent of the x-element described in diœcious forms.

In the maturation of the oogonia of fertile females ova are formed all of which have three chromosomes. The process of spermatogenesis, however, results in the formation of dimorphic sperms, half of which carry three chromosomes, and the rest two (see Fig. 5).

Now it will be remembered that fertilisation gives only females; this result, as Morgan and v. Baehr showed, is brought about by the degeneration of all the two-chromosome sperms. Fertilisation therefore is always effected by the union of three-chromosome sperms and ova, resulting in a six-chromosome zygote, which is potentially female.

The anomaly of the production of females only, from fertilised ova, is therefore satisfactorily explained, and brought into line with the phenomena in diœcious forms, by the discovery of the degeneration of the two-chromosome sperms, which are potentially male-producing. Thus the apparently homozygous male seems to be really heterozygous, but with its heterozygousness in a state of degeneration. The anomaly of the production of males and females by the supposed homozygous female is probably a real difficulty, but it will be best discussed after describing the cytological phenomena presented by the hornet and the bee.

The males of the bee and hornet develop from ova which have undergone reduction in maturation; hence follows the startling fact that all the cells of the male possess only the haploid number of chromosomes. Consequently the sperm-mother-cells of the bee or hornet have half the number of somatic chromosomes found in the female, and hence there is no need for a reducing division in spermatogenesis. In the latter process, however, the heterotype division does occur, but no nuclear matter passes into one of the products of division; and only one of the two potential spermatozoa, into which the other product divides, becomes, in the bee, a functional sperm, although both are functional in the hornet. Thus all the sperms retain the haploid number of chromosomes. These sperms, on fertilising eggs similar to those from which their producer arose, develop into females. The cytological details, however, have not been fully worked out, so that an interpretation of the bare facts is difficult, and is probably best postponed until more facts are known. The degeneration of three-quarters of the the sperms, however, leads us to infer, from the analogy of Aphids and *Phylloxera*, that the male bee or hornet is also a degenerate heterozygote.

The production of males and females by the female Bee, Hornet, *Aphids* or *Phylloxera*, however, cannot be explained on the assumption that the female is homozygous. It may be advanced that these specialised insects have acquired heterozygousness after acquiring parthenogenesis, that is, the power of producing males by spontaneous development after some sort of reducing division. But this is only a suggestion. There is little doubt, however, that, as a consequence of the acquisition of parthenogenesis, the male has degenerated from its original heterozygote condition to a virtual homozygote. Thus we are brought up sharply against the wall of evolution in our pursuit of Mendelian characters. Our surprise at the nature of the obstacle will diminish as we recall the importance of the Mendelian unit in other connections as a probable factor of evolution.

In reviewing the correlations in cytological and sex-phenomena in the cases just discussed, we may be justly permitted to infer that the male is heterozygous for sex with maleness dominant, and the female a homozygous recessive. Further, femaleness is always associated with two x-elements, and maleness with only one x-element or with one x- and one y-element. The y-element, it is found, may be present or absent in closely allied forms, hence, whether rightly or not, less importance is attached to it as a sex-determinant than to the x-element. Wilson has drawn attention to the close correlation in these phenomena between the haploid condition and maleness, and the diploid condition and femaleness. Herein would appear to be one of those curious differences which exist between animals and plants; for it appears that in plants the asexual spores are nearly always formed with the haploid condition of the chromosomes, and are nevertheless differentiated with regard to sex in certain Pteridophytes and all flowering plants.

I now pass on to consider another series of facts which support the view that the male is a Mendelian heterozygote. I refer to the sexual changes induced in organisms by the entrance of parasities into their tissues.

It is known that when certain fungi infest the region of the ovary in female plants of *Carex dioica* and *Lychnis dioica*, anthers develop. Analogous phenomena in animals have been carefully worked out; especially in the case of crabs and their parasites. G. Smith has observed[1] that when the Spider-crab is infested by parasites such as *Sacculina*, belonging to the group Rhizocephala, the sexual characters of both male and female undergo a profound change. The males, which are characterised by swollen chelæ, narrow abdomen and copulatory styles, change into a hermaphrodite condition by acquiring characters peculiar to the female, to wit, broad abdomen with swimmerets and smaller and weaker chelæ; indeed the male is, in its extreme condition, to be distinguished from the female only by the presence of copulatory styles. The female, on the other hand, very rarely loses its sexual characters and never acquires any of those peculiar to the male. Smith has examined the reproductive organs of infected crabs in all stages, and has found that if the crabs recover from the effects of the parasite (which they often do) the male may produce both mature sperms *and mature ova* in correlation with its acquired secondary sexual characters; but that the female produces ova only. Potts[1] has observed similar phenomena in other species of crabs.

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[1] Fauna and Flora of Gulf of Naples, Vol. XXIX., Rhizocephala.

Seeking to interpret these changes, Smith makes the suggestion that the sexual characters may depend not upon a differentiated reproductive organ, but upon a *sexual formative substance* which is defined as "a product of the general metabolism of the body which differs characteristically in the male and female." The parasites of the crabs interfere with the metabolism, whose product, the sexual formative substance, becomes changed, "causing in the female atrophy of the gonad and of the secondary sexual characters, in the male a passing from the highly differentiated male condition to the more generalised hermaphrodite state."

Smith does not ignore the indications of recent research, namely, that sex is probably fixed in the zygote: for he holds that "a legitimate distinction may be drawn between the presence of a metabolic substance in the body capable of assuming activity under the proper stimulus, and a transmission of a sexual potentiality which may depend on some quiescent structural element incapable of activity except after the elaborate and mysterious changes which accompany the inception of a new generation." Indeed he suggests that the male in these cases may be heterozygous for sex (DR) with maleness dominant, and the female a homozygous recessive (RR). Following up the idea that it is only the male which contains the potentialities of both sexes, Smith draws attention to the almost universal occurrence of protandric hermaphroditism in animals which have become secondarily hermaphrodite. This phenomenon is accounted for if it be assumed that, owing to a change in the habits of life, the sexual organs have undergone degenerative changes as a part of the general degeneration, and have become hermaphrodite in the one-time male. Many curious and unexplained sex-phenomena in the *Cirripedia* are explained very ingeniously by this theory.

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[1] Potts, Q. J. M. Sc. Vol. L., pp. 599-621.

A remarkable case of protandry in the animal world, *viz.*, in the slipper limpet, *Crepidula fornicata*, has been described recently by J. H. Orton.[1] This case illustrates and supports Smith's theory of the origin of protandry extremely well, inasmuch as *Crepidula fornicata* is a Mollusc which had diœcious ancestors and which both phylogenetically and ontogenetically has adopted a sedentary life—and hence tends to degenerate—and also presents every condition between the earlier, purely male, and the final, purely female, condition.

The observations on the phenomena of parasitic castration are thus seen to support the evidence derived from the Arthropods that the male is a Mendelian heterozygote and the female a recessive.

We are now in a position to compare the different conclusions which have been held with regard to a Mendelian interpretation of sex.

		Male.		Female.		
Castle	...	DR	...	DR	...	Plants and animals.
Correns	...	DR	...	RR	...	Some animals and plants.
Bateson	...	RR	...	DR	...	One plant and some animals.

Correns, it will be remembered, assumes a factor for monœciousness, which is recessive both to maleness and femaleness.

A study of the inheritance of sex indicates that for a number of animals and for one case among plants sexual phenomena are correctly described if the female be considered a Mendelian heterozygote and the male a recessive. On the other hand observations on cytological characters of a large number of Arthropoda, as well as the phenomena of parasitic castration in crabs, and the almost universal occurrence of protandry in animals,—all point to a gametic constitution the exact reverse of that just stated. The phenomena in parthenogenetic insects, however, indicate that a modification of Castle's view may be nearer the truth for these cases. It seems too much to expect that these opposite views can be reconciled. Indeed it is hardly likely that sex-phenomena will be unified in one scheme; for the evolution of differentiated gametes can be traced along several lines even in the lower organisms. It is therefore not reasonable to expect that sex should be inherited in the same manner throughout the animal and vegetable kingdoms. Indeed from the foregoing study of sex-inheritance, apart from the latter considerations, we should not expect males and females to be homologous throughout the whole organic world. Hence it is possible that the three Mendelian interpretations just mentioned may all be correct for some organisms; and, further, it is possible that sex may in some cases be found to be correctly described by assuming yet other gametic constitutions for male and female.

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[1] Proc. Roy. Soc. B., Vol. 81, 1909.

LECTURE VIII.

THEORY OF ANCESTRAL CONTRIBUTIONS IN HEREDITY.

IN my second lecture I dealt with an experimental test of the truth of the theory of heredity which I described as the theory of ancestral contributions. Professor Pearson, in a paper entitled "The Theory of Ancestral Contributions," published in the Proceedings of the Royal Society (B), Vol. 81, 199, p. 219, made the following criticism of these results.[1]

"Under the above title a paper has recently appeared by Mr. A. D. Darbishire . . . . . . giving further experimental evidence with regard to the inheritance of certain characters in Peas. The paper is an interesting one, but the method is not, I venture to think, capable of answering the problems the author set himself. It has been supposed by some Mendelians that the theory of inheritance summed up in the 'law of ancestral heredity' was in some way invalidated by investigations such as Mr. Darbishire's, and that opinion consciously or unconsciously seems to be expressed in the paper just referred to."

Professor Pearson was perfectly justified, it seems to me, in detecting an expression of this opinion in this paper as it stands; but as I do not hold it, I wish to explain how the misapprehension arose. The paper as it stands is no more than a bald statement of the experiment which I conducted, and was in its first form, preceded by somewhat lengthy exposition of what I meant by the theory of ancestral contributions. This preliminary discussion was not included in the paper as it appeared in the Proceedings of the Royal Society; and the fear, which I felt at the time, lest this omission should lead to misapprehension proved to be well founded.

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[1] Proc. Roy. Soc., Vol. 81, B, p. 61, et. seq.

I do not by any means hold that "the theory of inheritance summed up in the 'law of ancestral heredity'" would be invalidated by the result of the investigation which I conducted. Let me attempt to make my position clear.

The last twenty years have witnessed a gradual but profound change in our conception of the relation between successive generations of organisms. This revolution, which was initiated by the publication of Weismann's doctrine of the continuity of the germ-plasm, and is still far from being complete, consists in the substitution of the doctrine that new characters arise in the germ-plasm and, once arisen, owe their existence in subsequent generations to their existence *in potentiâ* in the germ-plasm, for the old view that characters arise in the soma and are in some way impressed on the germ-plasm to which that soma gives rise. So long as the older (in a sense, Lamarckian) view was held, the chief task before the student of heredity was to supply a hypothesis to explain how the character arising in the soma was transferred to the germ-plasm. It is not commonly realised how long this "Lamarckian" view of the question has persisted; nor how deeply it has been engraven on the imagination. That Darwin's conception of heredity was essentially of this nature is shown by the fact that his theory of Pangenesis was *par excellence* a theory to account for the transference of somatic characters from the soma to the germ-cells which it contains.

It is my thesis that the general view of heredity, in which biologists have tacitly believed, and on which practical breeders have acted, until the last few years, has been the natural outcome and immediate offspring of that conception of the relation between successive generations of organisms in which the mature individual occupies a primary and the germ-plasm a secondary position. According to this general view of heredity, which I have called the Theory of Ancestral Contributions, and shall subsequently refer to as the contributional view, or theory, the characters of an organism are composed of contributions from its several ancestors, the magnitude of the contribution varying directly with proximity of the contributing ancestor.[1] It is first necessary to prove that this has been the general view of the question. This will not be a matter of much difficulty. For it seems to me to be manifest that it was some such view as this which has led the breeder to confine his attention to the somata of the material with which he deals, and to believe that by breeding from individuals with a particular character for a sufficient number of generations, it is possible to "breed out" other, undesirable, characters. Further, there must have been *some* preconceived idea of heredity against which, as a sort of background, the facts of Mendelian inheritance appear striking and unexpected. And this preconceived idea was in my opinion the theory of Ancestral Contributions. For the fact that, for instance, the green individuals which reappear in F_2 from a cross between a yellow and a green Pea, produce nothing but greens (when mated together) in spite of the fact that both of their parents were yellow and that half of the sum total of their previous ancestors were also yellow, is only surprising to anyone who holds that the characters of an organism are determined by the somata of its parents and more remote ancestors.

As I have already said, the substitution of the Weismannian view for the contributional view of heredity is not yet complete. The process has, however, been much more rapid during the last eight years owing to the support which Weismann's doctrine has received from the facts discovered by Mendel and by those who have followed him. Still, even those facts have not sufficed to destroy a lingering faith in the old doctrine. They have, however, done what is better: they have narrowed down the issue by making it possible to deal with smaller and more specific problems. For instance, thanks to the knowledge which we now possess of the existence and (to some extent) of the nature of separately heritable unit-characters, I have been able to furnish a definite answer to the specific question whether there is anything like ancestral contribution within the limits of a single unit-character.

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[1] It is possible that the objection may be raised at this point that the principle which I have just formulated is none other than Galton's Law of heredity. This is not the case. I have shown elsewhere (*On the Difference between Physiological and Statistical Laws of Heredity*, Mem. and Proc., Manchester Lit. and Philosophical Society, Vol. 5, Pt. 3) that the controversy which followed the resuscitation of interest in the phenomena of Heredity by the rediscovery of Mendel's papers would not have taken place if a clear distinction had been drawn between statistical and physiological laws of heredity. Galton's law was a first attempt to reduce the chaos of hereditary phenomena to order; and this antithesis was naturally not before his mind. But if Galton's generalization be understood as a physiological theory applicable to individual cases, an interpretation which I do not think his own formulation of it warrants, the theory of ancestral contributions only differs from Galton's Law in that the exact amount of the contribution of each ancestor is specified in the latter; if, however, Galton's Law be understood as a statistical statement as to the composition of successive generation which is not true of the individuals which compose them, it has nothing to do with the theory of Ancestral Contributions.

But to return to the change in opinion which we have seen is taking place: the persistence of the contributional view amongst those who are not professedly Mendelian is most clearly proved by their attitude to two corollaries which follow from the interpretation which Mendel put on the facts which he observed.

The first of these concerns the ancestry of the parent forms used in the cross, and asserts that the offspring of the yellow hybrids produced by crossing a yellow with a green Pea will consist of 75% yellow and 25% green Peas *whatever the ancestry of the two parent forms is*, provided only that they are both homozygous.

The second concerns the posterity of the cross and asserts that the greens produced in F_2 are as pure as the pure greens started with, and, what is more remarkable still, that a green in (say) F_5 is equally pure. Those who still cling to the contributional view have grown familiar with the fact that such extracted greens do breed true; but they do not regard this fact as final proof of the Mendelian interpretation of this case, because they suspect that it may still be possible for these "green" germ-cells, which produce only greens, to contain an admixture of the yellow character without that character being manifested in the individuals to which they give rise.

The reader will remember that the result of the experiment proved that the ancestry of one of the two forms (both of which were homozygous) involved in the cross did not affect the ratios in F_2 in the way in which the theory of ancestral contributions would lead us to expect; and, further, that it was demonstrated that an extracted "green" belonging to F_5 is as pure a green as one which has bred true for many generations. It was, I think, unwise to express the conclusion to which I was led by the results of this experiment, in the statement that "ancestry does not make a difference," a statement which, as I have already pointed out, does not mean anything unless we make it clear whether we are referring to individuals or masses. To a biometrician, who is accustomed to think in terms of masses, the statement that ancestry does not make a difference is demonstrably false.

I ought to have said that my experiment demonstrated that, in the particular case dealt with, the characters of a given generation were determined by the potentialities existent in the germ-cells of their parents (as according to the Weismanno-Mendelian view); and not by the somatic characters of their parents and remoter ancestors (as according to the contributional view).

In a word, my "theory of ancestral contributions" is a term which I have coined in order to be able to refer briefly to the generally accepted view of the relation between successive generations of organisms, which the Weismanno-Mendelian view is gradually superseding. And a final demonstration of its falsity or correctness will not affect the Law of Ancestral Heredity as formulated by Professor Pearson one way or the other; though a demonstration of its truth would profoundly modify our attitude to the commonly accepted interpretation of Mendelian hereditary phenomena.

PROBABLE ERROR.

Attention to the exact numerical proportions, in which the various types dealt with in breeding experiments occur, has played a very important part in the progress of our knowledge of heredity. It is perhaps going too far to suggest that it was neglect to pay any attention to numerical proportions which prevented John Goss (who, as we have seen, observed the essential Mendelian phenomena) from enunciating the interpretation of them which we now associate with Mendel's name; but it is certain that an accurate record of these proportions was one of the conditions essential to the discovery which Mendel made.

In my fifth lecture I pointed out that many cases which, when first observed, were regarded as instances of the 1 : 2 : 1 ratio have been subsequently regarded as instances of the 3 : 9 : 4 ratio. Here again close attention to the exact numerical proportions themselves is necessary; for on it depends the answer to the question to which of these two types of ratio the particular case of segregation under observation belongs. Again, those who maintain that the theory of ancestral contributions holds good within the limits of a single unit-character would probably not contend that, for instance, the diminution of the proportion of the recessives in successive generations, as we proceed from the first cross, would be any more than a very small one in each successive generation; but they would be bound to maintain that such diminution took place. Now, in both these cases it is, of course, evident to the reader that the larger the number of individuals composing a given generation, the less will the interpretation based upon it be open to the objection that the difference between observation and expectation is due to chance ; that is to say, to the small number of individuals recorded. What we want to know, therefore, is how much the ratio determined from a generation of a given size may be expected to deviate, *on the average*, from expectation. Here statisticians come to our aid, and have provided us with a formula which enables us to estimate this.

Suppose that we have a hundred F_2 families, each one of which consists of a thousand individuals, the theory of probability does not lead us to expect that the determination of the proportion of recessives will be exactly 25% in each of these hundred families. On the contrary, basing our expectation on the theory of probability we should anticipate that if the frequency of the hundred ratios were plotted in the form of a frequency curve, such a curve would be of the normal type. The mean of this curve would probably near at 25% and the deviations would become less numerous as they increased in magnitude in the *plus* or *minus* direction ; and there would be a point on the base-line of the curve in the *plus* direction dividing the number of deviations in the *plus* direction into half, and a similar point, on the *minus* side of the mean, dividing the deviations in the *minus* direction into half. The value on either side of the mean, which divides the number of deviations on one side of the mean into two, that is to say the value corresponding to the point we have just been considering, is called the Probable Error.

But if each of the hundred F_2 families had consisted of 10,000 instead of 1,000 individuals, we should expect this point to be nearer the mean, that is to say, we should expect the deviations in this case to be smaller and to cluster more closely round the mean. In other words we should expect the Probable Error to be smaller. If, therefore, we can calculate this value beforehand for a generation of given size, we should expect half the ratios to fall inside the deviation indicated by this point, and half of them to fall outside. Now the only question of real interest is, how far outside the Probable Error deviations may be expected to fall, for as anyone who has dealt with the determination of such ratios will know, deviations can fall much further outside this point than they can on the inside, for on the inside they are limited by the mean. The general rule which statisticians employ is that *deviations very seldom occur at a distance outside the Probable Error which is more than four times as great as that between the Probable Error and the mean.* It should not, however, be forgotten that half the deviations are expected to fall outside and half inside the Probable Error; so that if a long series of results accord so closely with expectation that all of them fall inside the Probable Error there is ground for believing that they have been invented. The formula for calculating the Probable Error is as follows :—

$$\frac{100\left[0{\cdot}67449 \times \sqrt{a\left(1-\frac{a}{x}\right)}\right]}{x}$$

in which x is the total number of individuals (in the case of a Mendelian F_2 for instance); and a is the number (of recessives in the case under discussion), the Probable Error of whose percentage of the whole number is to be calculated.

Let me give an instance[1] in which the accordance between observation and expectation has been tested by means of this formula. The experiment in which I tested the theory of ancestral contribution consisted of crossing a pure yellow cotyledoned Pea with an "extracted" green one belonging to the F_5 generation, and in determining the ratio of greens in the F_2 derived from this cross. Eight different races of yellow Peas were employed in making these crosses, and the proportion of greens occurring in the F_2 generations derived from each of these yellow races was determined separately. They are given in the following Table, together with the actual number of yellows and of greens, the actual deviation from 25%, and the Probable Error in each case. The total F_2 has also been classified with regard to the ancestry of the green parent of the cross (the crosses having been made on three plants of different ancestry) so that the total F_2 may be sub-divided into eleven groups, eight being derived from classification according to the yellow ancestor of the cross, three according to classification by the green ancestor of the cross. In six of these eleven groups the deviation is in the *plus* direction, in five in the *minus* direction. It will further be seen that seven of the deviations (478, 479, 481, 482, 493, 483 and 484) fall within the Probable Error, and that the remaining four fall outside it, and finally that amongst these latter there is only one in which the deviation is greater than thrice the Probable Error, *viz.* 480, in which the actual deviation is a little over three-and-a-half times the Probable Error. This series of cases[1] shows therefore the kind of way in which observation may be expected to differ from expectation, and the deviations are just such as may be expected in a case of F_2 in which the proportion of 25% recessives obtains.

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[1] These results appeared in Proc. Roy. Soc., Vol. 81, B, p. 61, *et seq.*

Classification by yellow grand-parents:—

Catalogue number of grand parents.	Number of Yellows.	Number of Greens.	Percentage of Greens.	Actual Deviation of Percentage.	Probable Error of Percentage.
477[2]	14,081	4,532	24·35	—0·65	±0·212
478	7,172	2,405	25·11	+0·11	±0·299
479	20,761	6,951	25·08	+0·08	±0·176
480	3,978	1,224	23·53	—1·47	±0·397
481	2,777	942	25·33	+0·33	±0·481
482	11,140	3,715	25·01	+0·01	±0·240
492	14,157	4,658	24·76	—0·24	±0·212
493	1,408	486	25·66	+0·66	±0·677
—	75,474	24,913	24·82	—0·18	±0·092

Classification by green grand-parents:—

Catalogue number of grand-parents.	Number of Yellows.	Number of Greens.	Percentage of Greens.	Actual Deviation of Percentage.	Probable Error of Percentage.
483	38,565	12,788	24·9	—0·1	±0·129
484	17,150	5,719	25·01	+0·01	±0·193
485	19,759	6,406	24·48	+0·52	±0·179
—	75,474	24,913	—	—	—

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[1] First published in Proc. Roy. Soc., B., Vol. 81, p. 61.

[2] 477 is a native Chinese cultivated Pea. 478, a commercial German Pea. 479, this is the type of Pea sold for use with the peashooter and reached me through that medium. 480, a commercial Pea from Calcutta. 481, *Ditto* from Canada. 482, *Ditto* from Russia. 492, a yellow round Pea from Genoa. 493, a later sowing of the same strain.

I can, perhaps, bring this lecture to a close most usefully by giving the actual working out of the Probable Error in the case of one of these groups, namely, No. 477.

$x=18{,}613$ (*i.e.*, 14,081 + 4,532) $a=4{,}532$

$$\frac{a}{x}=\cdot 2435$$

$$1-\frac{a}{x}=\cdot 7565$$

$$a\left(1-\frac{a}{x}\right)=3428$$

$$\sqrt{a\left(1-\frac{a}{x}\right)}=58\cdot 55$$

$$\cdot 67449\times\sqrt{a\left(1-\frac{a}{x}\right)}=39\cdot 49$$

$$\frac{100}{x}\times 39\cdot 49=\cdot 212$$

Probable Error $=\pm\ \cdot 212$

THE FUNDAMENTAL UNITS OF VEGETATION:

Historical Development of the Concepts of the Plant Association and the Plant Formation.

By C. E. Moss, D.Sc.

Introduction.

THE subject of ecological plant geography has suffered and still suffers very considerably from a lack of uniformity in the use of its principal terms. This defect need not be a source of great wonder or surprise, as it obtains to a greater or lesser degree in all branches of knowledge, and more especially in the biological sciences. Many biological concepts possess an inevitable vagueness; and this is a reflection of the lack of sharply defined images in nature herself. So marked indeed is this the case that one suspects as artificial any classification of biological units which is capable of a rigid and determinate application. Taxonomy, the oldest of the branches of biology, has despaired of giving logically perfect definitions of the genus, species, and variety. It cannot be expected, therefore, that ecology, one of the youngest branches, shall do better with regard to the formation, association, and society; for the units of the plant-geographer agree with those of the systematist in being entities which are not invariably sharply marked off from each other in nature. Much, however, of the prevailing confusion in phytogeographical nomenclature lies less deeply seated than this; and to some extent, therefore, the malady is one of which hopes may be entertained of an ultimate, if not of a speedy cure.

The need of greater harmony in the use of terms in ecological plant geography was recognized at the International Congress of Geographers held at Berlin in 1899, and by the International Congresses of Botanists held at Paris in 1900 and at Vienna in 1905; and the matter is also to be considered at the forthcoming International Congress of Botanists to be held at Brussels in May, 1910. Warburg (1900), Flahault (1900-1901), Clements (1902), Olsson-Seffer (1905), and Gradmann (1909) have published papers dealing specially with matters of phytogeographical nomenclature; but their differing schemes and recommendations have not brought about the desired uniformity.

Warburg's suggestions were of a tentative and general nature, and referred to the nomenclature of groups of formations rather than to formations themselves. Flahault's suggestions were two-fold, relating, on the one hand, to "geographical and topographical units," such as regions and zones, and, on the other hand, to vegetational or "biological units," such as associations and formations. Clements' suggestions received a severe handicap in meeting with the immediate disapproval of Engler. Whilst it must be confessed that Clements' system was perhaps in some respects too elaborate to be workable, and that parts of it were undesirable on general grounds, it is to be feared that the prompt displeasure expressed by such an eminent plant geographer as Engler had the unfortunate and doubtless undesired effect of preventing certain other portions of Clements' scheme from receiving a fair and unbiassed consideration.

Recently, Warming (1909) has issued a book in English on the *Œcology of Plants*; and Professors Flahault and Schröter, in a leaflet circulated in connection with the forthcoming Congress at Brussels, have stated their opinion that this book solves nearly all the difficulties connected with phytogeographical nomenclature. It seems difficult, however, to support this opinion in the matter of Warming's use of the term formation; although, in certain other particulars, especially with regard to the use of the term association and with regard to the grouping of allied associations into formations, the opinion can be fully justified.

Perhaps too much stress has been laid by critics on the particular *terms* employed by plant geographers, and too little on the *concepts* which the terms were intended to convey; and the object of the present communication is to endeavour to trace the historical development of the harmonious elements now existing in the concepts relating to plant associations and formations, and to give to these general ideas those terms which historical and present day usage would seem to indicate as right and proper.

It must be remembered that, in the development of every branch of knowledge, a time occasionally arrives when it becomes necessary to expand a concept which for long has been attached to a particular term. A few years ago, for example, it was held to be desirable to extend the signification of the term seed so that it should be applicable to integumented megasporangia destitute of embryos. So long as the expansion of a concept is due to a real advance in knowledge, and so long as the broader conception is in harmony with the more fundamental aspects of the previous use of the term, the new use is not merely legitimate and desirable but absolutely essential, unless all branches of learning are to be overburdened with new terms whenever concepts undergo a necessary, logical, and developmental expansion.

THE PLANT ASSOCIATION.

The concept of the plant association is one of the oldest in plant geography. Without referring to the literature of the ancients, in which doubtless the germs of these concepts may be found, it is sufficient to say that, with regard to the plant association, the concept and the term were used by the illustrious Humboldt more than a century ago; whilst the term formation dates from the time of Grisebach (1838). Humboldt showed that he had a well-defined concept of the plant association even when he did not use the term, as the following passages illustrate (Humboldt, ?1806; Sabine's English tr., 1849: 264):—" In the temperate zone, and especially in Europe and northern Asia, forests may be named from particular genera or species, which, growing together as social plants, form separate and distinct woods. In the northern forests of oaks, pines, and birches, and in the eastern forests of limes or linden-trees, usually only one species of Amentaceæ, Coniferæ, or Tiliaceæ prevails or is predominant." After thus referring to *pure associations*, Humboldt continues with reference to *mixed associations*:—"Tropical forests, on the other hand, decked with thousands of flowers, are strangers to such uniformity of association ..... A countless number of families are here crowded together; and, even in small spaces, individuals of the same species are rarely associated." "The existence of a heath," according to another passage from Humboldt (1819: 295), "always supposes an association of plants of the family of *ericæ*." It is perhaps scarcely to be expected that the originators of great conceptions should always have kept them within consistent and logical bounds, especially when these conceptions were closely related to wider but, at the time, unformulated ideas; and it is not surprising, therefore, that Humboldt should occasionally comprise groups of associations within his term association. Thus it was, perhaps, when he wrote as follows (1807: 17):—"Les bruyéres, cette association de l'*erica* [*Calluna*] *vulgaris*, de l'*erica tetralix*, des *lichen icmadophila* et *hæmatomma* se répandent depuis l'extrémité la plus septentrionale du Jutland, par le Holstein et le Luneberg, jusqu'au 52ᵉ degré de latitude." In the same essay, Humboldt (1807: 15), after mentioning such plants as *Vaccinium Myrtillus*, wrote:—"Ces plantes associées sont plus communes dans les zones tempérées que sous les tropiques, dont la végétation moins uniforme est par cela même plus pittoresque." The modern concept of the plant association as well as the term may thus be traced to the works of Humboldt; and this concept and this term have, after many vicissitudes, come into very general use in the writings of modern ecologists and plant geographers.

Schouw (1822; German tr., 1823: 165) briefly mentioned a few plant associations, and invented a method of denoting them. To the stem of the generic name of the dominant plant of a pure association, he applied the suffix *-etum*. Thus a plant association whose chief constituent is the beech (*Fagus sylvatica*) he termed a Fagetum. Similarly Schouw referred to Palmeta, Pineta, Querceta, etc. Meyen (1836; English tr., 1846: 78, 80) spoke of Ericeta, Fageta, Oliveta (*sic*), Palmeta, and Pineta. This matter is important in more than its nomenclatorial aspect, a matter which is discussed later on in this paper, for it proves that the concept of the association, had become firmly established in the minds of plant geographers of different nationalities before Grisebach had enunciated his famous definition of the formation.

This definition was put forward in 1838; and, although

Grisebach's formation was wider than Humboldt's association, yet, from this date onwards, the term "formation" began to enter into direct competition with the term association. It is most interesting, however, to observe that the modern tendency is to retain the usage of the two great pioneers in so far as the term formation now denotes a vegetation unit more comprehensive than the association.

Not only has the term association had its rivals, but various concepts, quite foreign to the prevailing one, have at various times been attached to it. Lecoq (1855, iv.: 90, *et seq.*) spoke of the seasonal appearances (the "aspects" of Clements, 1905: 315, etc.) as "associations": thus, he referred to "associations du mois d'avril," "associations végétales du mois de juin," and so on. Loew (1879: 592) regarded as an "association" those species which entered a country at the same time; and Celakovsky (1869) is said to have used the term "formation" in this sense. Höck (1895: 227) also used "association" in the same way. Clements defined "association" (1904: 9) as "the coming together and the staying together of individuals," *i.e.*, "the arrangement of individuals in vegetation" (1905: 315). All these significations, however, have given way to the use of the term as a unit of vegetation of narrower limits than the formation, and characterized by minor differences in habitat and in floristic composition.

Blasius (1840-1; cited in Grisebach, 1846: 133) described certain plant associations (*sub nom.* "formations") in his account of Russian vegetation; for example, he spoke of a "dwarf birch formation," and a "formation of reed grasses and Carices."

Many of the "formations" of Kerner (1863, etc.) are also either associations or groups of associations.

Hult (1881, etc.) has described many associations ["formations"] in the vegetation of north Finland, such as an Empetrum "formation," a Nardus "formation," a *Betula nana* "formation," and a *Scirpus cæspitosus* "formation." Drude (1889: 25) considers that Hult's formations are too narrow, and terms them *Bestände*; and Warming (1909: 140) also rightly urges that this narrow use of the term "formation" is not exemplary, and that "it is better to speak of such smaller units as associations." Some of Hult's "formations" are perhaps only societies, *e.g.*, his *Poa annua* "formation" (1881: 53).

Kerner (1887-1891; English tr., 1895: 896) retained the term formation, although he regarded the selection of this name as not quite fortunate; "but, having been once introduced into the science, it must remain." On the whole, Kerner used the term "formation" in rather a narrow sense.

The "zones secondaires" of Masclef (1888 : 180, *et cet.*) may also be regarded as associations.

Drude's *Bestände (loc. cit.)* are vegetation units which are determined by the dominant or social species within a formation. Drude considered them as important units, and maintained that their study must yield a very accurate analysis of the vegetation. It may be here mentioned that the vegetation units which are indicated on the vegetation maps of British ecologists, are, on the whole, the *Bestände* of Drude. These are associations ; but whether or not the term *Bestände* may be legitimately used for all associations, including mixed associations, is not clear. However, Cajander (1903 : 23) distinguished simple, mixed, and compound *Bestände*. The term *Bestände*, in Drude's sense, has been adopted by many recent continental ecologists and plant geographers, such as Höck (1894, etc.), Schröter and Kirchner (1902), Cajander (1903), and Brockmann-Jerosch (1907).

Flahault (1896 : 450 ; etc.) has used the term association for many years. He tabulated (1896 : 309 ; 1897 : 22) associations of *Abies pectinata*, of *Pinus sylvestris*, of *Castanea vesca*, of *Quercus sessiliflora*, of *Fagus sylvatica*, etc., etc. ; and he has on many occasions described these and other associations. In 1900, he advocated the adoption of the term at the International Congress of Botanists at Paris ; and an English translation of his paper has been published (1901).

Schröter (1894), in an account of certain "associations de plantes" in Valais, described "formations" of *Festuca valesiaca*, of *Nardus stricta*, of *Carex sempervirens*, and so on : these "formations" are apparently associations in the modern sense of the term.

Graebner (1895, 1901) divided the heath formation of north Germany into "types"; and there can be no doubt that these, of which examples are Calluna heath, Tetralix heath, and Empetrum heath, are precisely what are meant nowadays by associations. Livingston (1905) took up the term "type," being apparently dissatisfied with the term "society" which he had previously (1901, 1903) used for what appears to be the same concept.

Robert Smith, one of Flahault's pupils, was the first to apply the term association to the vegetation-units of Great Britain. In the basin of the river Tay, R. Smith (1898) distinguished associations of *Fagus sylvatica* (introduced), of Quercus, of *Pinus sylvestris*, of

Betula, and of *Calluna vulgaris*. These were added to in his later memoirs (1900 a and b, 1905).

Schimper (1898; English tr., 1903-4) regarded "formations" either as "climatic formations" or "edaphic formations." Many of the latter, *e,g*., the Pes-caprae "formation," are associations (cf. Warming, 1909: 227, etc.).

Cowles (1899) followed Warming (1895) in rejecting the term "formation," and used the term "society." Cowles (1899: 111) defined his "society" as "a group of plants living together in a common habitat and subjected to similar life-conditions. The term is taken to be the English equivalent of Warming's *Plantesamfund*, translated into the German *Pflanzenverein*. The term formation, as used by Drude and others, is more comprehensive, in so far as it is not synonymous." It will be seen that this definition does not clearly distinguish between the association and the formation; but, on the whole, the "societies" described by Cowles (1899, 1901) are associations. The latter term has, however, recently been adopted by Cowles (1909, 1910).

It may be remarked that in Britain it is usual to employ the term *community* for a vegetation unit whose rank is not specified, like Warming's *Plantesamfund*, as in the sub-title—"an introduction to . . . plant-communities"—of Warming's new book (1909).

In the use of the term "society," Cowles has had a considerable following in America, among whom may be mentioned Livingston (1901, 1903), Whitford (1901), Brown (1905), and Transeau (1905-6). This is natural, as Cowles shares with Pound and Clements the great honour of being one of the pioneers of American ecological plant-geography.

Smith and Moss (1903), Smith and Rankin (1903), Lewis (1904), and Smith and Smith (1904-5) used the term association very cautiously, and the term formation scarcely at all.

Ganong (1903: 349, *et seq.*) divided the salt marsh formation of the Bay of Fundy into three associations, namely, a Spartinetum, a Salicornietum, and a Staticetum. Ganong's concepts were clear, and his terms unequivocal.

Cajander (1903: 24) regarded as comprised within the same association all those *Bestände* in which the same species is dominant; thus, all pine *Bestände* would belong to the same association. It is perhaps doubtful if this view is quite correct; for certain communities which are characterized by the same dominant species sometimes occur on different habitats, and are accompanied by very different dependent species. For example, it is difficult to believe that British beechwoods on the Chalk belong to the same association as those on the Greensand.

W. G. Smith (1904 : 620) held that the "nomenclature of ecological plant geography, in spite of attempts to systematize, is at present too chaotic to attempt an exact definition of the terms used . . . . . For the present, it is safer to designate associations by prefixing the names of the dominant plants . . . . . . The smaller associations may be designated by plant names, *e.g.*, Juncetum, Caricetum, Psammetum, etc., or by prefixing generic and (in some cases) specific names, *e.g.*, Molinia association, *Juncus squarrosus* association, etc."

Pethybridge and Praeger (1905) based their work on the recognition of associations, which they arranged into "zones." In the moorland "zone," they described, among others, associations of *Calluna vulgaris*, of *Vaccinium Myrtillus*, of *Scirpus cæspitosus*, and of *Eriophorum angustifolium*.

Olsson-Seffer (1905) stated that a formation may be subclassified into associations and these again into "communities," the latter being indicated by the termination *-etum*.

Clements (1905 : 295-6), on very unconvincing grounds, used a new term "consociation, or better consocies," for the concept of the plant association. There is, however, no doubt as to his meaning; for he stated that his "consocies, under the term association . . . . . . have been recognized for several years." There appears no likelihood that Clements' new term will come into general use; but it must be stated that Clements' concepts of the formation and its primary subdivisions were perfectly well-defined, and in thorough accord with modern usage.

Hardy (1905 : 45) accepted the definition of the association given by Pavillard (1905), who was quoted to the following effect:—"Une association végétale est un groupement spontané, un peuplement naturel où les unités spécifiques, généralement étrangères les unes aux autres, vivent côte a côte, avec le profit exclusif de chacune pour objet, mais où des formes biologiques très différentes peuvent être juxtaposées et même subordonnées entre elles, suivant la diversité des exigences satisfaites par les conditions du milieu modifié ou non par les organisimes concourants." This definition, from the standpoint of the modern subdivision of the formation into associations, is rather vague.

Brockmann-Jerosch (1907 : 248-9, etc.) divided his formations into associations; but his use of the terms appears to me to be rather inconsistent. With regard to woodland communities, his "formations" are rather narrow and circumscribed, like those of Hult. For example, Brockmann-Jerosch speaks of "formations" of *Castanea vesca* [*C. sativa*], of *Pinus sylvestris*, and so on. These units are, in my judgment, associations; and they were so treated by Flahault (*op. cit.*). It is significant that Brockmann-Jerosch does not subdivide these narrow woodland "formations" into associations; but that wider formations, such as "Sumpfwiese," he is able to analyse into associations, such, for example, as associations of *Phragmites communis* and of *Molinia coerulea*.

Moss (1907) was the first among British ecologists to speak both of formations and associations. Thus, the sand dune formation of Somerset may be subdivided into progressive associations of strand plants (*Atriplex* spp., etc.), of sea-couch grass (*Agropyrum junceum*), of marram grass (*Ammophila arenaria*), of dune sward-forming plants, of dune pasture plants, and of dune marsh plants. Similarly, in the acidic peaty moorland formation of the Pennines, stable associations of *Calluna vulgaris* and of *Eriophorum vaginatum* may be distinguished, and also retrogressive associations of such species as *Vaccinium Myrtillus*, *Empetrum nigrum*, and *Rubus Chamaemorus* in varying proportions.

Warming (1909: 139, *et seq.*) followed what has become the general practice of subdividing the formation into associations. The latter he defined (p. 145) as follows:—"An association is a community of definite floristic composition within a formation." This point of view may now be regarded as having become all but universal; but it would be better to refer to the minor differences of habitat as well as to the differences of floristic composition in all definitions of the association. By so doing, the main object of the study of vegetation would be emphasized; and a tendency—by no means an imaginary one—to regard plant geography as a branch of floristic botany would be checked. It is perhaps overbold for a science that is still only in its infancy to state that it depends upon "mere accident" whether one or other of these associations prevails at a given spot (Warming 1909: 140), especially as, in many instances, these minor differences in habitat may be actually demonstrated.

It will be seen that the concept of the plant association, and also the term, have been long established, and that they have come to be very widely accepted among ecologists and plant geographers of several nations. Although for a time the term was threatened by the term "formation," and although many other terms have been used to convey the same general idea, and the term has been used to denote other concepts, yet the original term of Humboldt, and in the general sense used by Humboldt, meets with wide acceptance at the present time. It is true that Humboldt's concept has been expanded, as he appears to have had no notion of uniting allied associations into a group of wider significance; but such a classification of associations was ultimately inevitable. It appears likely that the term association, in the general sense here indicated, will be submitted for adoption at the International Congress of Botanists shortly to be held at Brussels; and one hopes that its adoption will be effected. A firm if small step will then have been taken in the direction of the unification of the use of phytogeographical terms; although the precise degree of relationship between the formation and its associations may not be fully realized for some time to come.

THE PLANT FORMATION.

The concept of the plant formation is, in a general way, much older than the term; for whilst the latter only dates from Grisebach (1838: 160), the former may be found in the writings of several of the pre-Linnæan botanists. The foundation of the idea of the formation, as understood by many recent writers, is the habitat; and from this point of view therefore it is fair to trace, as was done by Clements (1904: 12), the modern concept of the formation back to the old idea of the general habitat, even though the early systematists failed to realize fully the vital relations of habitat and vegetation. Linnæus, in his *Philosophia Botanica* (1751: 263-270), distinguished twenty-five habitats, and mentioned their characteristic genera; whilst in the *Stationes Plantarum* (1754; 1760: 64-87) the characteristic species were enumerated. Many of these habitats and accompanying lists of species might easily pass muster as a summary of the corresponding modern plant formations; and one is therefore tempted to speculate as to what would have been the relationships of the branches of modern botany had Linneæus developed this concept on the vegetational rather than on the floristic side. As it is, whilst the general habitat of the early systematists has become the formation of the plant geographer, it has long been the species-station of the taxonomist.

Even earlier than Linnæus, Tournefort (1717, iii.: 178, *et. seq.*) had more than an inkling of ecology when he distinguished the vertical belts of vegetation in Armenia, thus proving, according to Clements (1904: 150), that "the concept of zonation is the oldest in phytogeography."

It was shown in the preceding section of this paper that the term "formation" has frequently been used to signify an association. Clements (1905: 292) has stated that "there have been as many different opinions in regard to the application of the term formation as there are concerning the group which is to be called a species;" and Flahault (1901: 405) also wrote: "It is not to be marvelled at that several botanists, who had doubtless lost their way in this confusion, acknowledge having employed the word without thinking of its definition."

It is not surprising, therefore, that the development of the concept has proceeded along somewhat divergent lines. One such line has already been indicated: this was the use of the term by Hult (1881, etc.) and others to signify a minor though important unit of vegetation, a unit which is now regarded as a subdivision of a formation, and termed an association. A second line of development may now be traced.

An oft-quoted passage of Grisebach (1838: 160), introducing the term "formation," is thus rendered by Clements (1905: 3):—"I would term a group of plants which bears a definite ["abgeschlossenen"] physiognomic character, such as a meadow, a forest, etc., a *phytogeographical formation*. The latter may be characterized by a single social species, by a complex of dominant species belonging to one family, or, finally, it may show an aggregate of species, which, though of various taxonomic character, have a common peculiarity; thus, the Alpine meadows consist almost exclusively of perennial herbs." It is obvious that this general statement of Grisebach's early idea of the formation does not exclude all associations, for many of the latter "bear a definite physiognomic character" and are "characterized by a single social species." Hence those writers, such as Hult, who have used the term "formation" in the narrow sense, *i.e.*, as equivalent to an association, are able to find some historical support for their procedure. On the other hand, it must be admitted that the particular units of vegetation to which Grisebach applied his term were almost invariably of greater extent than single associations.

A review by Grisebach (1849: 339, *et seq.*) of a work by Duchartre (1844) enables one to gather the meaning which the eminent plant-geographer attached to the term in his earlier writings. Duchartre himself does not appear to have used the term formation, although his divisions ot the vegetation prove that he held the concept quite sharply. Grisebach in his review applies the term to Duchartre's divisions, thus speaking of the formation of the dunes, of the salt-water marshes, of siliceous soils, of calcareous soils, of argillaceous soils, etc. Such a use of the term was frequently adopted by Grisebach (cf. 1846 : 73 ; etc.) about this time ; and one sees that here Grisebach regarded the formation and the habitat as indissolubly connected. However, in his classical work *Die Vegetation der Erde* (1872), the term is used to denote physiognomical units, such as tundra, and the forests of definite geographical regions, which most later authors agree in subdividing into smaller units. Hence, practically every author, however he may use the term, may find some support for his procedure in one or other of the writings of Grisebach. The greatness of Grisebach must not lead us to regard his masterly concept as a fetish ; and the analysis of his "phytogeographical formations" into more definite vegetation units is a necessity demanded by the more rigorous methods of modern phytogeography.

Perhaps the most usual application of the term formation by present-day investigators is closely akin to the one which Grisebach held to in 1846 and 1849 ; and from this point of view a plant formation may be regarded as the vegetation co-existent with a definite habitat.

Several of the "associations" of Lecoq (1854, i : 291, *et seq.*) are either groups of associations or formations.

Kurz (1870), in a report on the vegetation of the Andaman Islands, classified the vegetation into divisions which, to some extent, correspond to formations, and subdivided these, in some cases, into associations, although Kurz does not use these or any other special terms. He described the vegetation (1) of the shores, (2) of the coasts, (3) of the high forests of the interior parts, (4) of the woodless spots, (5) of the cleared lands, and (6) of the sea. Some of these he subdivided into smaller units. Thus, the vegetation of the coasts is subdivided into (a) evergreen forests, (b) deciduous forests, and (c) bamboo jungles. The evergreen forests are further subdivided into (1) "kuppalee" (*Mimusops indica*) forests and (2) mixed forests ; and these are associations.

In his account of the forest and other vegetation of Pegu, Kurz (1875) divided the vegetation of that region into evergreen forests, deciduous forests, bamboo jungles, savannahs, natural pastures, riparian vegetation, freshwater vegetation, saltwater vegetation, etc. Several of these groups of plant-communities are further subdivided; for example, the evergreen forests are subdivided into littoral and other forests, and the littoral forests themselves into mangrove jungles and tidal jungles.

Two years later, Kurz (1877) described the forests of British Burma in a masterly way which has elicited the commendation of Drude (1889: 27). In none of his works did Kurz use the special terms formation and association, though he held the concepts clearly. His forests were separated mainly by habitat. Thus he distinguished (1) littoral forests, (2) swamp forests, (3) tropical forests, (4) hill forests, (5) open forests, (6) dry forests, (7) mixed forests, (8) dune forests, and adds, as an appendix, (9) bamboo jungles and savannahs, and (10) deserted clearings. These units are in some cases subdivided. Thus, the hill forests he subdivided into (a) deciduous forests and (b) coniferous forests; and these he further subdivided. Thus, the coniferous forests provide pure associations (though Kurz does not use the term) of *Pinus Kasya* and of *P. Merkusii.*

Although Kurz avoided the use of special terms in the description of his vegetation units, it is impossible to deny that he had clear concepts not only of formations and associations, but that he also understood, in some measure, the relations of these vegetation units to each other.

In the interesting account of the vegetation of northern France by the abbé Masclef (1888), the concepts of the formation and its associations may also be found. This account is like those by Kurz in that the terms formation and association are not used; but Masclef evidently found some terms necessary, or at least desirable. He accordingly termed his vegetation units "zones" and "zones secondaires"; and these, in a general way, correspond to formations and associations. Thus, Masclef, described a "zone marine," a "zone des vases," a "zone des falaises," a "zone des eaux sumâtres," and a "zone des dunes." Masclef had a follower in de Lamarlière (1894), who, in a short account of the maritime vegetation of de Quineville (Manche) stated (p. 137):—"On y retrouve les mêmes zones établies par M. Masclef et si bien étudiées par lui, et elles son caractérisées par les mêmes espèces communes."

To Drude (1889) modern plant geographers are greatly indebted for a clear (and perhaps the earliest) formulation of the concepts of the formation and the association, as well as the application of these general ideas to the vegetation of definite districts. He expressed

(p. 29) dissatisfaction with Grisebach's physiognomical definition of the formation, and held that whilst this might serve to distinguish classes of formations, a precise idea of the formation can only be obtained by taking into account the floristic composition. As there is a definite relation between habitat and the total floristic composition, this aspect of the formation may be regarded as in accordance with much of the later work of ecological plant geographers. Drude applied his general ideas to the vegetation of the Hercynian hill-country of Central Europe, which he subdivided into twenty-seven formations. These he then subdivided into associations; for example, the halophyte formation (p. 48) he subdivided into "Salzsumpf-Bestand," "Salztrift-Bestand," and "Trockne *Salsolaceen*-Flur." In connection with the descriptions of British moorland associations, the "montane Grassmoor-Formation (Warming)" is especially interesting. This formation (p. 44) Drude subdivided into the following associations:—"Sumpfwiesen-Bestand," "Binsenmoor-Bestand," "Wollgras- und Riedmoor-Bestand ("Grünmoore")," and "Torfsumpf-Bestand"; and the first three of these appear to be very closely related to some of the associations which occur on British upland peat moors. Although Drude at the outset of this communication stated that his object was the deepening of floristic studies, he by no means overlooked the importance of the habitat. He laid down (p. 28) the general principles that formations should be based on all conditions of existence (soil, water, atmospheric moisture) and on the associated species, and that the alternation of various principal and subordinate species within the same formation gives rise to the various associations (Bestände).

Warming (1895: 3-10) was so impressed with the confusion which had overtaken the term "formation" that he recommended its disuse. The wider meaning Warming thought might be indicated by the word vegetation; and for a plant-community of no assigned rank he used the term *Plantesamfund* (Pflanzenverein). The term "formation," however, had become so firmly rooted in ecological and phytogeographical literature that even the weight of Warming's authority was insufficient to cause its extirpation; and the trenchant treatment of the "formation" by Drude in the following year (coincident with the appearance of Knoblauch's German translation of the *Plantesamfund*) gave the term a new lease of vitality.

In his *Deutschlands Pflanzengeographie* (1896), Drude again emphasized the habitat, and stated (p. 281) that the plant-covering of a country is expressed in the arrangement according to definite habitats and coincides with the alternation of the principal plant associations (" Pflanzenbestände "). On p. 286, Drude defined the conception of the "formation" which he held at that time as follows :—" Any independent principal association, which has found its natural termination in itself, which consists of similar or of biologically connected plant-forms, and which is confined to a locally determined substratum of similar conditions of maintenance (altitude, exposure, substratum, water supply) has the value of a vegetation formation,—it being assumed that no actual change of association would occur on the site of such a principal association without external changes : the association has " reached its term " [" abgeschlossen "] " (cf. Warming, 1909 : 143).

As a definition of a closed, ultimate, or *chief association* of a formation this statement of Drude's is excellent ; and there can be no doubt that Drude's arrangement of the different forests of Germany into fourteen " formations " is a great advance on the merely physiognomical view ; though, as his " formation " is essentially only a particular kind of association, it is not quite consistent with the views of those authors who regard the formation as related to the association as the genus is to the species. There may be associations which are also formations, just as certain genera only contain a single species ; but probably such formations are less frequent than monotypic genera.

Schimper (1898, 1903 : 160, *et seq.*) laid the proper emphasis on the fundamental relation between the habitat and the formation. He stated (p. 161) that " every formation is in its floristic and ecological character a product of climate and soil."

Pound and Clements (1898 ; 1900 : 314) wished to preserve Drude's concept of the formation ; but their subdivision of " the river bluff *formation* " into " (1) the red oak hickory *formation* " and "(2) the burr oak elm *formation* " (pp. 324-333 [italics mine]) does not tend to clearness of thought.

Cowles (1899 : 111) propounded a view which has become widely adopted when he compared the formation with the genus and the association (" society ") with the species. Cowles stated his view as follows :—" One might refer to particular sedge swamp societies near Chicago, or to the sedge swamp formation as a whole : by this application, formation becomes a term of generic value, plant-society of specific value."

Ganong (1903 : 300, *et.seq.*) regarded the salt marsh associations with which he was dealing as subdivisions of a larger unit, the wild salt marsh formation; and his treatment therefore of the formation which he so closely studied was strictly in accord with the usage which was becoming more and more general. His formation was obviously determined by habitat, his associations by floristic composition and minor differences of the general habitat.

Harshberger (1904), in a phytogeographical sketch of a portion of Pennsylvania, subdivided formations into associations. He determined his formations and associations by the character of the land on which they occur (p. 133), *i.e.*, by habitat. However, many of his "associations" (cf. p. 145) are undoubtedly units which British authors would term only societies.

Although many earlier writers regarded the formation and the habitat as vitally connected, it is to Clements (1905) that ecologists owe the most emphatic expression of this view. Clements (1905: 292) stated unequivocally that "the connection between formation and habitat is so close that any application of the term to a division greater or smaller than the habitat is both illogical and unfortunate. As effect and cause, it is inevitable that the unit of the vegetative covering, the formation, should correspond to the unit of the earth's surface, the habitat." This view, as has been shown, was by no means new; but no one had previously stated with sufficient emphasis and in general terms what must be regarded as the foundation of the modern treatment of vegetation. The concept is much more stimulating and much more scientific than a merely physiognomical view of the formation; and this latter view, useful enough in the early days of plant geography, has now been quite outgrown. It is no longer possible to regard a forest as a "formation," nor even a coniferous forest. Such complex pieces of vegetation must be resolved into separate associations, and the latter rearranged into formations on a basis which shall commend itself to those who search after real affinities and underlying causes. The rearrangement of associations into formations will not be accomplished at once, except in the case of well-marked habitats. Where the habitats are less sharply defined, much exact and quantitative experimental work remains to be done; and here again Clements, in his *Research Methods in Ecology*, has performed useful and pioneer work. Until much work of this character has been performed, until certain habitats have been more closely investigated, ecologists and plant-geographers must be content to refer certain communities simply to their associations, rather than hastily build up formations on flimsy foundations.

Clements' treatment of the subdivision of the formation is also on the main line of development, for his primary division of this unit is the association, termed by him the "consocies."

The floristic view of the formation put forward by Brockmann-Jerosch (1907: 237, *et seq.*) has recently found an exponent in Gradmann (1909); and their views may therefore be considered together. Whilst these authors recognize that formations should be subdivided into associations, they think that the best way of delimiting formations is by their floristic composition. "One begins to record," wrote Gradmann (1909: 99), "as completely as possible, and in as many places as possible, the natural closed[1] plant-communities as one finds them in the country. It soon appears that certain single associations have much more in common with each other than with all the others. They can be united into groups, and each of these groups makes a formation of closely allied single associations. The formation comprises in this case all the species of the single associations belonging to it, and thus appears as an abstraction, in that it is not easily realized in a single narrowly limited locality, but only by considering the whole extent of all the associations belonging to it."

Whilst nearly, if not quite all modern ecologists and plant geographers will agree most cordially with this ultimate concept of the formation as composed of allied associations, it does appear that, in cases where formations are characterized by well-marked habitats, the method of delimiting the formation by the method outlined by Gradmann is, in some cases, unnecessarily circuitous. It is surely superfluous to have to draw up full lists of species in order to decide whether one is examining a sand-dune, or, peradventure, a peat moor! Even Clements, than whom no one has more strongly insisted on the necessity of examining the factors of the habitat, states (1905: 293) that "this test of a formation is superfluous in a great many cases, where the physiognomy of the contiguous areas is conclusive evidence of their difference."

Gradmann does not overlook the possibility of determining formations by habitat; for he says (p. 96) that "since necessarily each formation must correspond with definite habitat conditions, it is quite conceivable that we can give adequate diagnoses simply with the help of habitat conditions for all the formations of a region ..... This would be an ecological diagnosis of which one certainly could not deny the scientific value." Thus, as Gradmann agreed, this aspect of the formation is on a very different level from the physiognomical one or even the "ecological" one on the basis of water-content alone.

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[1] Why should the investigation be limited to *closed* associations?

Whilst the goal reached by the two methods—by the *floristic* method advocated by Gradmann and by the *habitat* method advocated in this paper—must in all cases be the same, the latter method would appear to be the more appropriate, and indeed the more fundamental, from the point of view of the study of vegetation as distinct from the study of the flora. The study of vegetation is not a department of taxonomy. Each is a separate department of science, although it is true that a knowledge of the latter is essential to a study of the former. The view advocated by Gradmann should not, in my judgment, supersede the view that the formation must be determined primarily by an investigation of the habitat; but Gradmann's method furnishes an auxiliary and confirmatory test of the formation in all cases of doubtful habitats. I fully agree that no formation can be properly described without giving a full list of its species. I would go further, and insist that such lists must include the characteristic "elementary species" of the formation, for these are frequently much more characteristic of formations than the well-defined species; but to insist that the floristic composition of the formation is more important than the habitat is to maintain that effect is more fundamental than cause.

Moss (1907) followed many previous authors in delimiting formations primarily by habitat, and then subdividing the formations into associations. Applying the test of habitat to the natural and semi-natural woods of Somerset, he distinguished habitats which are characterized respectively by woods of oak (*Quercus Robur* = *Q. pedunculata*), of ash (*Fraxinus excelsior*), and of oak and hazel (*Q. Robur* and *Corylus Avellana*). More extended observations in other parts of the country (cf. Moss, Rankin, and Tansley, 1910) prove that the "oak-hazel woods" of southern England belong to two different communities, one characteristic of non-calcareous clays and derived from woods dominated by *Q. Robur*, and another characteristic of calcareous clays and marls, and related to woods whose dominant tree is *Fraxinus excelsior*. The latter woods are characteristic of many kinds of calcareous soils in England, but do not appear to have been described by continental writers. In the Peak District of Derbyshire, woods of *Quercus sessiliflora* are sharply marked off from woods of *Fraxinus excelsior*: the former are strictly confined to siliceous hill slopes, and the latter, with equal strictness, to hill slopes on the Carboniferous Limestone. Whatever view be taken of the influence of calcium on plants, a matter on which physiologists have no definite information to offer, there can be little doubt that the woods of *Quercus sessiliflora* and those of *Fraxinus excelsior* are related to special habitats and are characterized by distinctive species, and that they should therefore be placed in separate formations. To place these communities in the same formation because they possess the same "definite physiognomical character," or because they are characterized by the same plant form, is to obtain a blurred concept of vegetation and to obscure the relations of vegetation and habitat.

Following Warming, Graebner, Cowles, Clements, and others, this writer laid stress on the succession of plant associations, especially on *the succession of associations within the same formation.* Clements (1904, 1905) had previously discussed the phenomena of succession at some length, and had brought out most clearly its importance in vegetation. It is necessary, however, to distinguish the series of associations within a whole succession, that is, the succession from one formation to another, and the succession of associations within one and the same formation; and Moss (1907 : 12) enunciated a statement of the formation from the latter point of view.

Succession of associations within a formation may be either progressive or retrogressive. In the salt marshes of the south of England, for example, a succession of *progressive associations* of Zostera, of Spartina, of Salicornia, etc., culminates in a comparatively stable association of close turf formed of *Glyceria maritima.* The latter association, however, may be attacked by the waves and ultimately destroyed; and thus *retrogressive associations* are produced. In the case of established woods, we do not know the progressive associations which culminated in the woodland associations; but we can determine retrogressive stages through scrub to grassland. Similarly, the retrogressive associations which are seen in denuding peat moors are recognizable.

A plant formation, then, comprises the progressive associations which culminate in one or more stable or *chief associations*, and the retrogressive associations which result from the decay of the chief associations, so long as these changes occur on the same habitat.

It sometimes happens, as in the case of the peat moors on the Pennine watershed, that the original habitat is wholly denuded and a new rock or rock-soil surface laid bare. In other cases, as when sand dunes are built up on the site of a pre-existing salt marsh, a habitat may be overwhelmed by a new one. In such cases, the succession passes from one formation to another formation. Again, a new habitat is created when an open sheet of water becomes choked up with silt and peat. It is absurd to dignify every stage in this succession by the term "formation"; and it is equally absurd to regard the vegetation of the open water as belonging to the same "formation" as the vegetation of the peat moor. Taking a wide view of this succession, it is obvious that the series of associations has passed from one formation to another. There is less difficulty than might be expected in delimiting the formations in such a succession, as is proved by the success of the existing Ordnance maps of such localities as the Norfolk Broads. Without any special ecological or botanical training, the makers of these maps distinguish, and distinguish successfully, between an aquatic formation (which they map as water) in which is included the reed swamps, and the fen formation (which they map as land) which begins where the reed swamps end. The succession, in such cases as these, passes from one formation to another.

The above examples of succession are given in order to show the importance of regarding the formation from the point of view of its developmental activities; but this point of view, like that of Brockmann-Jerosch and Gradmann, cannot supersede the view that the formation must be primarily determined by habitat. It cannot be successfully maintained that the view which I here put forward introduces into the concept of the formation any more subjectivity than it at present contains; for, since the stages of the conversion of a shallow "mere," "broad," or lake into a "moss," "fen," or peat moor are gradual changes, and since no one would include the earliest of such stages in the same formation as the last, there is therefore, at present, a certain degree of arbitrariness in deciding which of the various stages shall be included in one formation and which shall be included in another. It is, of course, quite obvious that no system of scientific nomenclature is possible which is not, in some of its aspects, more or less subjective.

From the point of view of succession, the "formation" of Drude (1896 : 286), variously termed by him "Formation," "Hauptformation," and "Haupbestand," must be regarded as a *chief association* of a formation. The chief associations of a district, however, do not comprise the whole of the vegetation of that district: they serve to give a vivid, but to some extent an impressionist picture of such vegetation; and the complete picture requires the addition of the details provided by the progressive and retrogressive associations, or, as these may be collectively termed, the *subordinate associations*.

Every formation has at least one chief association: it may have more; and they may be regarded (*cf.* Drude, *loc. cit.*) as equivalent to one another in their vegetational rank. They are more distinct and more fixed than progressive or retrogressive associations. They are usually, but not invariably, closed associations. They always represent the highest limit that can be attained in the particular formation in which they occur, a limit determined by the general life conditions of the formation. In desert and sub-glacial regions, the chief associations are open; and, in such cases, it is legitimate to speak of open formations. Open progressive and retrogressive associations, however, frequently occur in formations whose chief associations are closed. On a British salt marsh, for example, open progressive associations of *Salicornia annua* frequently occur, while the chief association of *Glyceria maritima* is closed; and similarly on a Pennine peat moor, open retrogressive associations of *Vaccinium Myrtillus* occur, whilst the chief associations of *Calluna vulgaris* and of *Eriophorum vaginatum* are closed. Unless, however, the progressive and retrogressive associations are included in the same formation as the related chief associations, an incomplete or an unbalanced picture of the vegetation results. Cowles (1910) has used the term "climatic formations" for those vegetation units which I regard as chief associations. Cowles' term is peculiarly unfortunate, as it is used in a very different sense from the same term of Schimper's.

It is maintained that the view of the formation which is here advocated is more likely to be productive of valuable results than any view which allows of the delimitation of plant formations merely by physiognomy or by plant form. It concentrates attention on the habitat and on the relation of this to the plant covering; and it cannot be denied that the superficiality of much ecological work is due to the neglect of investigation of habitat conditions. At the same time, the view is essentially in harmony with the floristic view of the formation of Brockmann-Jerosch (1907) and of Gradmann (1909), since, in general, the floristic composition is a result of the habitat conditions; but it differs from their view in regarding the plant covering of a habitat more from the vegetational standpoint than from that of the flora, and in thus keeping more in line with the historical development of ecological research.

Warming (1909) has recently adopted the term formation; but he has given the concept an unfortunate bias. However, in subdividing his formation into associations, he has taken up a view which has forced itself on the minds of nearly all close students of of vegetation. Warming (p. 131, *et cet.*) compares the formation with the taxonomic genus and the association with the taxonomic species. It follows, as many others had previously maintained, that a formation includes a number of allied associations.

Cowles (1909: 150) in reviewing Warming's (1909) book has again emphasized his view that the "conception of a formation as an ecological genus and an association as an ecological species is now becoming generally accepted in principle; but this concrete statement by the father of modern ecology should make its acceptance universal." If therefore the Congress at Brussels should adopt this view, a second firm step will have been taken towards unifying the concepts and terms of ecological plant geography.

Warming's view of the formation itself, however, is sufficiently at variance with historical and present-day usage to demand some examination of his treatment of this unit of vegetation. Confusion is apparent even in Warming's summary statement of the formation. The latter, he stated (1909: 140), may "be defined as a community of species all belonging to definite growth-forms, which have become associated together by definite (edaphic or climatic) characters of the habitat to which they are adapted." Thus, instead of a single *fundamentum divisionis*, Warming puts forward two tests, namely, definite plant forms ("growth-forms") and definite characters of the habitat, of the formation. It is not clear, either from his definition or from his general treatment of formations, what Warming precisely means by the term "definite growth-forms." Does he mean that a plant formation is characterized by a single plant form, by a single dominant plant form, or by a single set of different but biologically connected plant forms? In any case, the definition is defective, as plant form is not necessarily related to habitat; and therefore the two tests put forward in the one definition will frequently yield contradictory results. It would appear that Warming himself felt this difficulty; for, in spite of his definition, he also stated (p. 142) that "it is nature of locality that must be represented by formations." Yet Warming insisted (p. 232) that a salt marsh characterized by suffruticose Salicornias "must be set apart from" salt marshes characterized by herbaceous Salicornias "as a separate formation," merely because the plant form in the two cases is different. Such paradoxes occur throughout the whole of Warming's book; and indeed this Janus-like "formation" is inevitable if plant form be allowed to enter into competition with habitat in the determination of formation. Warming's view might find some justification if definite plant forms were invariably related to definite habitats; but it is quite certain that this is not the case. For example, on salt marshes in the south of England, it is no unusual thing to find associations characterized (a) by herbaceous species of Salicornia, (b) by suffruticose species (*S. radicans* and *S. lignosa*), and (c) by a mixture of these. To place these associations in separate "formations," however, simply because of the different nature of the plant forms, is to reduce the study of formations to an absurdity.

This criticism is not intended to convey the meaning that the study of plant form is not desirable or even essential. On the contrary, such a study in the hands of ecologists and plant geographers has led to most useful results. It must, however, be emphasized in Warming's own words (1909: 5, 6) that "we are yet far distant" from the "ecological interpretation of the various growth forms," that "it is an intricate task to arrange the growth forms of plants in a genetic system," and that among growth forms "it is difficult to discover guiding principles that are really natural."

It is to be regretted that Warming has made so unfortunate an experiment at a time when the delimitation of the formation by the habitat was becoming generally adopted; and it seems clear that the Brussels Congress should not recommend a view of the plant formation that has not yet been shown to be capable of a logical or consistent application. Apart from Warming's new book, a clear lead, however, was distinctly indicated; and, in my judgment, the Congress would be justified on the grounds both of historical and present-day usage, in ignoring that element of Warming's definition of the formation which refers to plant form, and in recommending for adoption the view that the formation should be determined primarily by habitat. If the Congress cannot undertake this step, it seems clear that the matter should for the present remain in abeyance.

METHODS OF DENOTING ASSOCIATIONS AND FORMATIONS.

Whilst Schouw's plan (1822, 1823: 165) of referring to an an association by the suffix *-etum* is simple and brief, it has its imperfections. In the first place, it does not distinguish the species of the dominant plant, but only the genus to which the species belongs. The plan is particularly ambiguous in the case of such genera as Juncus, Quercus, and Pinus, each of which contains several species which are dominant in unrelated associations.

Cajander (1903 : 23) has a modification of Schouw's plan, which, to a large extent, overcomes this difficulty; and Cajander's plan appears to meet with Warming's approval (1909: 145). By this method, an association of *Juncus effusus* is not referred to merely as a Juncetum, a term which might refer to an association of *J. glaucus*, or of *J. maritimus*, or of *J. obtusiflorus*, or of *J. squarrosus*, and so on: Cajander's plan is to add as a genitive the specific name of the dominant plant of the association. Thus an association of *J. effusus* would be a Juncetum Junci effusi, or more briefly, a Juncetum effusi; and similarly an association of *J. maritimus* would be a Juncetum maritimi.

A second objection applies equally to Schouw's plan and to Cajander's modification of it. Neither method is applicable to mixed associations, which have no single dominant species. Of course, some characteristic species might, in certain cases, be utilized; but this would be arbitrary and unscientific, and in some cases, perhaps, impracticable.

The designation of a pure association by its dominant species is a very different matter from determining the association by such a species. Against the latter superficial method of determining associations Drude has expressed himself on several occasions; and recently Gradmann has emphatically condemned such a procedure. The naming of a pure association, however, by its dominant species is comparable with the plan of naming a systematic group after an easily recognizable character; and in neither case does such a name exhaust the characters of the group it denotes.

With regard to denoting particular formations, Clements' plan (1902: 16; 1905 : 299) is comparable with the one propounded by Schouw for denoting associations. Clements has put forward a number of terms, each with the termination *-ium*, to denote various classes of formations (1902: 5). As this suffix would easily lead to confusion with neuter generic and specific names, I here modify it to *-ion*, a termination which is now obsolete in taxonomic names. Thus modifying Clements' terms, a *Cremnion* (κρημνός) denotes a cliff formation, an *Eremion* (ἔρημος) a desert formation, an *Oxodion* (ὀξώδης), a sour bog formation, and so on. These terms Clements would make more definitive by the addition of the generic names of the plants which are dominant in the associations of the formations. Taking the Oxodion as an example, if this formation consisted only of two associations dominated respectively by *Eriophorum vaginatum* and *Scirpus cæspitosus*, the formation would, on Clements' system, be denoted by the term "Eriophorum-Scirpus-Oxodion." This name would not, however, be really definitive; as no indication would be given of the species of Eriophorum or of Scirpus which are the dominant plants of the two associations; and the range of habitat and of form in these two genera is considerable. Nor do such terms as "magno-Caricetum" and "parvo-Caricetum" (Schröter, 1904: 49) overcome this difficulty in the least. Further, the Oxodion comprises not merely two associations but probably at least two dozen. In the British Isles alone, there are, in this formation, associations of *Calluna vulgaris*, of *Empetrum nigrum*, of *Eriophorum angustifolium*, of *E. vaginatum*, of *Molinia cærulea*, of *Vaccinium Myrtillus*, and others. Add to these, the various other associations of this formation known and described on the continent of Europe alone, and the designation of the formation by Clements' plan reaches Brobdingnagian proportions.

Two other criticisms may be made of Clements' scheme as it stands. Clements uses the same suffix for formations determined by habitat, and for formations classified by a totally different principle. Thus, the same suffix is used to denote open, initial, mixed, intermediate, ultimate, and closed formations; and the same suffix is used also to denote succession; yet these concepts are quite distinct from that of the formation as determined by habitat. However, these are matters capable of adjustment.

There is, in my judgment, so much to be said on general grounds in favour of a universal language for the designation of formations that this point need not be argued; and, although the particular terms chosen by Clements may not be the best of all possible terms, it seems clear that many of them are eminently adapted for the purpose for which they were intended. The fundamental weakness of Clements' plan is the inclusion of generic names in the designations of formations; and this inclusion does not appear to be necessary. It seems sufficient to denote the formation by a single word, *e.g.*, Oxodion, whose termination would mean formation and whose root, and, if necessary, also a prefix, would indicate the habitat. The advantages of such a plan are that the technical term used to denote the formation would remain brief or comparatively so, that it would emphasize the habitat, and that it could be used in connection with an associational name framed on the plan of Cajander. Thus, an association of *Eriophorum vaginatum* belonging to a formation characterized by a sour peaty soil could be indicated by the term Oxodion Eriophoreti-vaginati.

The question of universal names for vegetation units is bound up with that of the universality or otherwise of particular formations. Of course, whenever climatic differences are sufficiently strong to be related to a radically different vegetation, then it is obvious that a different formation has been produced; for climatic factors no less than edaphic factors assist to form the habitat. Similarly, differences of flora may be related to differences in geographical position; and the latter too must be regarded as an element, or rather as a complex of elements, of the habitat. Whilst the geographical position of the Pennines is sufficiently different from that of Connemara in the west of Ireland to bring about certain differences in floristic composition, these differences are scarcely sufficient to justify the placing of the peat moors of the Pennines in a different formation from the peat moors of Connemara.

Following Cajander (1903: 24) and Warming (1909: 145, *et. seq.*), differences of this character may be said to bring about *varieties of associations*, which are the "facies" of some authors.

With regard to peat moors of America and those of Europe, however, the geographical position is doubtless sufficiently different in the two cases to justify a formational separation; and this would seem to be demanded whether the formations be determined by habitat or by floristic composition. Such formations should certainly be correlated into groups of allied formations; and the resemblances of the edaphic factors of the habitats in question would necessitate such a grouping in any cosmopolitan treatment of formations. In a system of universal nomenclature, such affinity could be indicated by some prefix. For example, an Oxodion in one climatic or geographical region might perhaps be termed an α-Oxodion, and another Oxodion in a different region a β-Oxodion, and so on.

Warming, however, apparently places in the same "formation" many communities which differ widely in geographical position and wholly or almost wholly in floristic composition. For example, he places in his "formation" of "succulent steppe" both the bushland in Morocco composed of species of Euphorbia and the communities of plants which occur on the plateaux of Texas and Mexico, even though in the latter locality "are found species absent from the old World, including those of Agave, Yucca, and, above all, Cactaceæ" (Warming, 1909: 279).

It is not proposed to offer here a list of such formational and associational designations, as nothing can be more certain than that an acceptable language is never evolved on such a ready-made plan. Even the binomial system of Linnæus was not altogether a novelty; and it would probably have been rejected by the botanists of the day, had it been propounded prior to the Tournefortian plan which it superseded.

I suggest, however, that ecological writers and phytogeographers, when describing particular formations and associations, should suggest such universal names for them in addition to the more colloquial names which are at present in use. The technical or universal name would not supersede the common or colloquial name; just as *Bellis perennis* is still known as the daisy, and just as trichlormethane is still known as chloroform. The need of a universal terminology in the designation of formations and associations has, however, become acute; and it seems to me that, if prejudice be put on one side, the basis of such a common tongue may be found in the plan here outlined. If a universal scheme be wholly rejected, phytogeographers must remain content with their present inchoate terminology.

The objection that such names as I have suggested are clumsy is of no more weight than the similar objection which might be urged (and indeed frequently is urged by non-specialists) against similar terms used by systematic biologists and by chemists; and the grea value of the latter terms is beyond argument.

GROUPS OF FORMATIONS.

It is obvious that allied formations may be arranged into still more comprehensive classes. Every phytogeographical monographer, in fact, has arranged his formations in some order; but very few have claimed for these higher groups the value of natural divisions. For example, the majority of such authors have arranged their formations or associations into groups which followed the ancient division of the vegetable kingdom into trees, shrubs and herbs; but it is scarcely possible that such a basis can ever yield a scientific or natural classification of plant communities; although Warming (1909: 140-141) makes this "the prime basis of classification" in subdividing the groups of hydrophilous, xerophilous, and mesophilous plants. One finds too that authors have adopted points of view which differ according to the size and extent of the earth's surface which they happened to be investigating; and this perhaps is inevitable. It is the same in taxonomy. Those systematists who have dealt with continental areas or with whole phyla of plants have invariably given a wide significance to the species; and those who have studied intensively the flora of small districts, or who have monographed special genera, have generally used the term species in a much narrower sense.

Many of the physiognomical "formations," *e.g.*, tundra, of Grisebach and others, are to be regarded either as groups of formations or groups of associations; and these may or may not be natural groups. Kerner (1863) arranged his minor "formations" into groups (Gruppen von Genossenschaften). Drude (1890) in his *Handbuch*, in which he dealt with the whole world, adopted a physiognomical classification on the whole: in his *Deutschlands Pflanzengeographie* (1896), his "formations" (chief associations) were arranged into groups some of which depend largely on physiognomy, *e.g.*, wood "formations" and scrub "formations," and others largely on habitat, *e.g.*, moor "formations" and aquatic "formations;" whilst in his still more detailed study of the formations of the Hercynian region (1899), he adopted a more natural classification and one based more completely on habitat.

Warming's (1895) classification of plant communities, to some extent based on the work of Schouw (1822, 1823), was undoubtedly the most fundamental which had at that time been put forward. Warming based his major divisions, hydrophyte communities, xerophyte communities, halophyte communities, and mesophyte communities, on the nature of the habitat, partly on the water content and partly on the mineral content of the soil. This classification, however, met with some adverse criticism, particularly with regard to the inclusion of "bog xerophytes" among hydrophytes, with regard to the separation of halophytes from xerophytes, with regard to the inclusion of all conifers among xerophytes and of all deciduous trees among mesophytes (cf. Stopes, 1907; Moss, 1907b: 6), and with regard to the group of mesophytes in general. This appears a somewhat formidable indictment; but the fact remains that, at the time, Warming's grouping was the best constructive effort which had been put forward in the direction of a natural and scientific classification of plant communities.

Schimper's (1898) division into hygrophytes, xerophytes, and tropophytes was in several respects superior to the earlier one put forward by Warming.

Schimper's "climatic formations" are doubtless, in general, groups of formations; whilst others may really be formations. As Clements (1904: 27), Smith (1904: 620), and Warming (1909: 132) have maintained, it is undesirable to separate those habitat factors depending on climatic conditions from those depending on edaphic conditions. Still, with regard to certain districts, such as the rainier portions of several tropical countries, whose vegetation and flora, partly from lack of exploration and partly owing to certain inherent difficulties, are little known, such "climatic formations" as tropical rain forest are at present the only practicable vegetation units. Kurz (*op. cit.*) has, however, indicated that the classification of even tropical forests will yield ultimately to more intensive treatment; and it seems clear that many "climatic formations" must ultimately be analysed into formations. With regard to well-worked countries, there is, from the standpoint of an ultimate and natural grouping of plant communities, nothing whatever to be said in favour of regarding as "formations" such complex groups of associations as deciduous forests, coniferous forests, grassland, and so on. For example, it can scarcely be contended that Warming's "formation of deciduous dicotyledonous forest" (1909: 144 and 329) is of the same rank as his "low moor formation" (p. 196) or his "high moor formation" (p. 200); and the real difficulty is only temporarily shelved by subdividing highly heterogeneous "formations" into "subformations" of little less heterogeneity.

The new classification of formations into higher groups by Warming and Vahl (1909) is much more involved, and much less simple and clear, than Warming's earlier one; and it is very doubtful if the changes have resulted in any gain in accuracy. Already it has met with some adverse criticism by Cowles (1909: 151), Tansley (1909: 221), and Moss (1909: 351) in their respective reviews of Warming's new book (1909). In particular, the "ecological class" of coniferous formations has been singled out for criticism. "Whilst this group," says Cowles (*loc. cit.*), "is a floristic unit, ... it is far from being a geographical unit of any sort. It would seem better to put many conifers with the lithophytes and psammophytes, whilst others are certainly oxylophytes, and others still pronounced mesophytes, the most mesophytic forests of the United States being dominated by conifers." Several closely allied formations are, in my judgment, placed apart by the first divisions of Warming and Vahl's new system. It must be remembered too that many plants, *e.g.*, "bog xerophytes," possess some organs which, considered by themselves, would result in these plants being termed hydrophytes, whilst other organs would result in their being termed xerophytes; and certain plants, such as deciduous trees, are extreme xerophytes during winter, yet possess leaves which are "mesophytic" during summer. Hence it is to be feared that any attempt to place every plant in a verbal class with the termination *-phyte* is either impossible or premature.

Graebner's (1901, 1909) classification of plant formations into larger groups has much to recommend it. Graebner (1909) makes three main divisions:—

(*a*) Formations where the soil-water is rich in nutritive salts.
(*b*) Formations where the soil-water is poor in nutritive salts.
(*c*) Formations where the soil-water is saline.

These main divisions are further subdivided chiefly on the basis of the water-content of the soil, and then still further subdivided by other physical factors. Thus the formations themselves are ultimately reached. This classification, although its author, of course, makes no claim that it is final, is, on the whole, and within an area of fairly constant climatic conditions, a natural one because it takes into account the whole of the factors comprising the habitat, and because no conflicting factor, such as plant form, is introduced. Doubtless future research will suggest some emendations; but it may be regarded as the most successful of the existing systems, and as planned on a general and scientific basis which will lead to ultimate success.

Gradmann (1909: 93) has maintained that, in the matter of classifying formations, plant geographers should be given full liberty. It is sufficient to point out that plant geographers, have, in the past, exercised such liberty; and the result is chaos.

CONCLUSION.

I should have liked, had space permitted, to have also traced the development of the concepts of those minor units of vegetation which are subdivisions of associations. These are important from two points of view. First, they are the outstanding vegetation units to the student of vegetation who is investigating the detailed structure of a very limited area. That such intensive studies may yield results of great value is seen from a perusal of such works as those of Woodhead (1906) and Brockmann-Jerosch (1907), and from unpublished results by several British ecologists. It is becoming usual in this country to speak of the subdivisions of the association as plant societies (cf. Clements, 1905: 296). Graebner (1895, 1901) and some other continental ecologists have termed them "facies"; but the term "facies," like the term "society," has been used in several other senses. In fact, so many terms have been used by ecologists and plant geographers with so many different significations that it would appear to be impossible to find any term to which the above objection does not apply. The intensive study of plant societies permits of a rigorous and quantitative determination of habitat factors, as has been done by Hedgcock (1902), Livingston (1906), Yapp (1909), and others, and in unpublished work by Professor Oliver, Mr. Crump, and Mr. Adamson. Woodhead's useful generalisation with regard to "competitive" and "complementary" communities (1906: 396, 7, etc.) is also an outcome of this kind of work. Such work also lends itself to the investigation of the physiological responses of plants to definite habitat factors. The latter work has scarcely been begun by ecologists; but it is certain that a rich reward of results awaits investigators who undertake such research.

Secondly, the investigation of plant societies is necessary to the study of the formation; for several writers have displayed an unfortunate facility in mistaking the one vegetation unit for the other. Pound and Clements, Drude, Clements, and others have protested against the tendency of certain writers to elevate to the rank of a formation any phase of a succession or any slightly different patch of vegetation. This tendency has to be guarded against in all intensive studies of vegetation; and the *quasi* definiteness of the local patches of vegetation in a restricted area can only be corrected by comparative observations in other districts.

The study of vegetation needs workers from all the departments of ecology and plant geography indicated in this paper. The monographers of the wider areas have still to concentrate attention on a natural grouping of formations, the investigators of the very restricted areas on the factors of the habitat and on the responses made by the vegetation to these factors. Formations themselves require to be carefully delimited; and the associations of each formation need detailed study from the points of view of zonation, alternation, succession, and floristic composition. The study of vegetation touches on physiology at many points, but at present there is not and cannot be any essential identity between them: it needs the systematist, but it is in no sense a branch of taxonomy. Vegetation must be studied from the standpoints of its development, its structure, and its activities; and the object of this study is the elucidation of the relationships of vegetation to the factors of the habitat.

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ON THE CAUSES OF THE ZONING OF BROWN SEAWEEDS ON THE SEASHORE.

II.—The Effect of Periodic Exposure on the Expulsion of Gametes and on the Germination of the Oospore.

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As was stated in a previous paper on this subject (New Phytologist, Vol. VIII., p. 196, 1909), it seems probable that the most important physical factor governing the zoning of Brown Seaweeds is the periodic exposure by the tides. In order to find out, as far as possible, why some species grow high on the shore and others lower down, it is necessary to work out in detail the effect of exposure on the different species. Some experiments on the effect of periodic dessication on vegetative growth have already been described (*loc. cit.*); the work described in the present paper was carried out with a view to determining the influence of this factor on the germination, and also on the dehiscence mechanism of the four species under observation. Some details are added on the mode of expulsion of the gametes from the conceptacles.

Except where otherwise stated, all these experiments were carried out at White Cliff Bay, Bembridge, Isle of Wight, during July and August; and were made, as far as possible, on the seashore.

The order of zoning observed on the shore was as follows:—(1) *Fucus spiralis*, L. (=*F. platycarpus*, Thur.) (2) *Ascophyllum nodosum*. (3) *Fucus vesiculosus*. (4) *Fucus serratus*; beginning from the high water line and going downwards.

I.—Effect of Periodic Dessication on Germination.

To obtain ripe gametes, receptacles of both kinds were left dry for a few hours, and then put into filtered sea-water. The water containing the eggs and sperms was mixed and left standing twelve hours to ensure fertilisation; it was then divided equally between three straight open glass tubes, the lower ends of which were covered with filter paper protected by muslin on each side. The tubes were provided with wire hooks by means of which they could be hung inside glass jars of filtered sea-water, and so be filled with water. As soon as the tubes were removed from the water it ran out through the filter paper, leaving the young plants dry; the last few drops of water were expelled by blowing into the tops of the tubes. The plants were left dry, and in water, alternately for definite intervals of time; thus imitating the periodic exposure by the tides.

The results of four weeks' treatment may be summarised as follows:—

In water 11 hours, dry 1 hour, in every twelve.

The plants of all four species were at about the same stage of development, most of them had a much divided rounded thallus with a well-developed branched pseudopodium, and a few hairs at the top of the thallus. In all the species certain specimens had reached only about the eighth division, and occasionally the thallus was perfectly round, without any development of a pseudopodium.

In water 6 hours, dry 6 hours, in every twelve.

The specimens of *Fucus spiralis* and *Fucus vesiculosus* were at nearly the same stage as in the former case; most of them having the much divided round thallus, occasionally with hairs, and attached by a well-developed pseudopodium. There were, however, specimens which had only divided about eight times and even only once or twice. The plants of *Ascophyllum nodosum* were at an earlier stage, the most advanced specimens showing seven divisions; while in the tube containing *Fucus serratus* no plant was found showing more than four divisions, and many had only divided twice. The pseudopodia were well developed in all these.

In water 1 hour, dry 11 hours, in every twelve.

The specimens of *Fucus spiralis* had many of them divided three times, though others showed only one division. The most advanced specimen of *Fucus vesiculosus* had three divisions, another had divided once, and several were not divided. The pseudopodia were well-marked in both these species. No germinated specimens were found in the tubes containing *Fucus serratus* and *Ascophyllum nodosum*, though several undivided oospores were found.

It appears from these results that the species occupying the highest zones can germinate, and become attached under all conditions; but those growing in the lower zones will not germinate under the tidal conditions obtaining in the highest zones. It is noteworthy that *Fucus vesiculosus* behaves in this connection, as though it occupied a higher zone than *Ascophyllum nodosum*, which is the reverse of the order found on the shore in this locality.

II.—EFFECT OF EXPOSURE TO THE AIR ON THE EXPULSION OF GAMETES FROM THE CONCEPTACLES.

The first essential is to have a means of measuring the number of reproductive bodies ejected from a definite number of conceptacles under various conditions. The method employed was as follows. The specimens were collected as the tide ebbed, whenever possible, and were left in a large rock pool until required. They were then carefully washed, and exposed to the open air, by leaving them lying on flat stones on the shore, for definite periods of time. The dried receptacles were covered with a measured quantity of water, after trimming them so that there were 200 conceptacles in each receptacle. After twelve hours the receptacles were removed and the number of bundles of gametes in the water was counted. The bundles of oospores were sufficiently large to be fairly easily counted with the naked eye, or a small lens, when the water was contained in a white glazed vessel. The number of bundles of antherozoids was estimated by taking out, with a pipette, several drops of approximately the same size (after violently stirring the liquid) and counting the number of bundles in each drop under the microscope; the mean value of three readings has been used in every experiment. The weights of ten consecutive drops of pure water, delivered from the same pipette, were found to vary from 0·0197 gram to 0·0229 gram per drop, the mean value being 0·0213 gram; so the variation in volume of drops is not more than about 16%. The pipette used to measure out the water was a short one with a fine capillary just above the bulb, so that the liquid adjusted itself mechanically to a definite level in the capillary, by means of surface tension. This enabled several small quantities of water to be accurately measured out in a very short time. The volume of the pipette used was found to be 3·348 ccs. which is about 160 times the volume of one drop. This method of counting the numbers was employed in all the experiments referred to in this paper except where otherwise stated.

The methods are open to several errors:—

(*a*). Errors in counting; these are extremely easy to make when the numbers involved are large, and can only be avoided by care and system.

(*b*). Errors due to breaking up of the bundles of gametes can be obviated to a certain extent in the case of the oospores, which can be roughly counted; and the number of bundles broken up is then estimated by dividing by eight for the *Fuci* and by four for *Ascophyllum*.

(*c*). Errors due to insufficient stirring and variation in size of drops in the measurement of the dehiscence of the male conceptacles.

Besides these a still more important source of error was found to be the variation in ripeness of the individual specimens, however carefully they were chosen. The only possible method of getting over this was to take a number of readings with different specimens for each experiment, and use only the mean value. The number of readings taken was, however, not sufficient to prevent this source of error from being a serious one.

The results of a series of experiments carried out to ascertain the effect of different durations of exposure on the four species is given below in tabular form. The numbers for the oospores indicate the number of bundles ejected from 200 conceptacles. The numbers for the bundles of sperms indicate the mean numbers found in one drop, *i.e.*, $\frac{1}{100}$th the number ejected from 200 conceptacles, or approximately the number from one conceptacle. The values under the headings "O" were obtained by leaving the seaweeds in water for ten hours, then transferring them to fresh sea-water and leaving them twelve hours, and then counting the number of bundles ejected.

I.—*Fucus serratus* ♂.

Hours Dry ...	4	3	2	1	½	0
Experiments	78	21	118	45	29	43
	27	54	13	14	8	12
	21	23	7	—	12	77
	24	—	23	—	10	22
	—	—	—	—	54	—
	—	—	—	—	56	—
Means	37	33	38	29	28	38

Fucus serratus ♀

Hours Dry ...	9	3	2	1
Experiments	187	67	64	28
	151	140	72	52
	171	240	—	18
Means	169	145	68	33

II.—*Fucus vesiculosus* ♂

Hours Dry ...	9	6	1½	½
Experiments	8	8	8	4
	—	—	—	3
Means	8	8	8	4

Fucus vesiculosus ♀

Hours Dry ...	9	6	3	1½	½
Experiments	59	133	64	76	27
	90	97	56	58	33
	230	103	68	39	41
	54	—	124	64	—
Means	108	111	78	59	34

III.—*Ascophyllum nodosum* ♂

Hours Dry ...	6	5	4	3	2
Experiments ...	10	8	4	4	1

Ascophyllum nodosum ♀

Hours Dry ...	4	3	2	½
Experiments ...	61	59	21	0

The experimental methods were varied in the case of this alga. Six or seven receptacles were covered with two measures of water, after counting the number of conceptacles, and the results reduced to the values for 200 conceptacles and one measure.

IV.—*Fucus spiralis* ♂

Hours Dry	24	14	9	6	3	1	0
Experiments	12	20	18	1	7	3	9
	19	20	11	3	2	4	3
	13	10	11	6	4	2	4
	5	36	14	6	4	1	7
Means	12	23	13	4	4	3	6

Fucus spiralis ♀

Hours Dry	24	14	9	6	3	1	0
Experiments	138	264	207	35	90	80	61
	203	174	158	92	27	64	67
	312	147	89	73	76	74	29
	127	420	323	99	118	33	62
Means	195	251	194	74	78	63	54

The values for the bundles of eggs and sperms were found from the same specimens in this species. The experiments have been so arranged that a given specimen occupies corresponding positions in both tables. It is to be noted that the specimens giving many oospores give also, as a rule, many sperms; apparently both kinds of gametes ripen at about the same time. The mean values have been plotted graphically against the time of exposure (Fig. 1). It will be noticed that the curves are all very similar in shape. At a certain point there is a rapid increase in the number of bundles liberated with time of exposure, followed by an approximately constant value varying very little with the time. It looks as though a certain length of time of exposure was required to make the mechanism efficient, and this appears to vary with each species. In the diagram the points at which the mechanism may be said to become efficient have been indicated by arrows for each species; in the case of *Ascophyllum nodosum* the experiments were not carried far enough for this point, if it exists, to be reached. The length of time required for efficiency increases progressively as the seaweeds grow

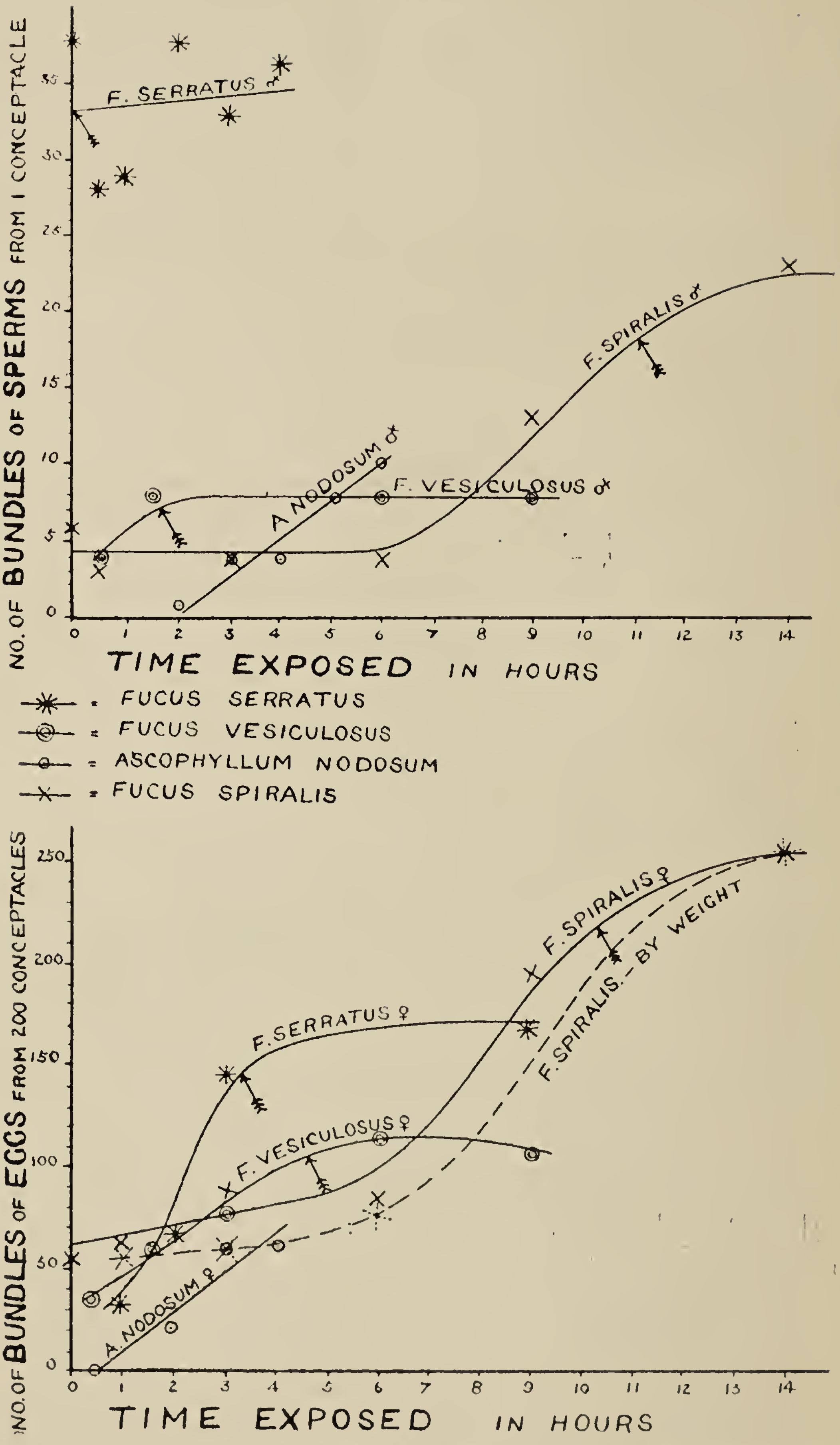

Fig. 1. Diagram illustrating the variation in the number of gametes expelled, with time of exposure. The arrows indicate the points at which the dehiscence mechanism of each species may be considered to have become efficient. The dotted curve represents the proportional values found for *Fucus spiralis* by weighing the gametes.

higher and higher on the shore; the order being the same as that of the zoning observed. It is noteworthy that *Ascophyllum nodosum* is the only species in which exposure to the air appears essential to the expulsion of gametes; in all the Fuci considerable dehiscence takes place even when they are not exposed, though the maximum efficiency may not have been reached. The experimental methods are, however, not sufficiently trustworthy to do more than to indicate the probabilities for the intermediate species, and to contrast the behaviour of the two extreme species. It will be remembered that the receptacles of *Fucus serratus* are only very slightly swollen, while those of *Fucus spiralis* and the other two species are enlarged and filled with mucilage, so that for *Fucus serratus* a short time of exposure would be as effective in drying as a much longer exposure for the other species.

III.—Observations Connected with the Method of Expulsion of the Bundles of Gametes.

Farmer and Williams (Phil. Trans. B. (1898), 190, p. 629-631), Oltmanns (Beiträge zur Kenntniss der Fucaceen. Bibl. Botanica 3, 14, 1-19), Thuret (Ann. d. Sc. Nat., Bot. IV., 2, 197-214), and others have shown that the bundles of gametes are extruded by means of the mucilage which collects in drops at the openings of the conceptacles, when they are exposed to the air. It should be noticed that this effect appears to be much more marked when the receptacles are exposed to a very moist atmosphere, than when they are left lying in the sunshine and wind, as was the case in the present experiments. On the shore, as Peierce has pointed out (Torreya, Vol. 2, No. 9, p. 134-136) the plants tend to lie over one another and so keep the air round the receptacles fairly humid; this makes it difficult to imitate the real conditions of the shore.

Farmer (loc. cit.) has also suggested that the long paraphyses occurring in the conceptacles play a part in the dehiscence mechanism. A chance observation led to the suspicion that this effect had, if anything, been underrated. A section was cut through the ostiole of a very ripe ♂ conceptacle of *Ascophyllum nodosum* which had been exposed overnight. After covering the section with sea-water and a glass, the ejection of about 20 bundles of spermatozoids through the ostiole was observed during a period of about half-an-hour. It was noticed that each bundle moved, from its point of attachment, between two of the paraphyses; also that its movement was by a series of irregular jumps, and further that beyond the region of paraphyses, which project a little way out of the ostiole, no further motion occurred. It appeared as though the ejection was caused by the swelling up of the adjacent paraphyses on being put into water, the bundles moving in the direction of least resistance away from the point of attachment of the paraphyses. Although several hundreds of sections of receptacles in various stages of dryness have been cut, this phenomenon has not since been observed. One bundle of sperms has been seen moving by jerks in *Fucus vesiculosus*, and two on different occasions in *Fucus serratus*, but not more.

It was thought advisable to try the effect on the dehiscence of removing some of the paraphyses. The hairs were removed by putting the receptacle into a liquid, allowing the liquid to solidify (thus embedding the projecting paraphyses) and then pulling off the solid mass which contained the hairs. *Fucus spiralis* was used for the experiment, since in this species the paraphyses project in large tufts from the conceptacles. The first liquid used was paraffin wax. The receptacle was dipped into molten wax, then at once put into cold water, and the loosened shell of wax removed with a penknife. Some of the paraphyses which were only dragged partly out of the conceptacles, and were still attached to small pieces of wax, could be easily cut off with a sharp knife. In order to eliminate, as much as possible, the error due to a different degree of ripeness in the receptacles, the twin receptacles formed by the dichotomy of the thallus were used; one being waxed and the other being similarly treated, only without the waxing. It was found that the waxing was only efficient in removing the projecting paraphyses when the receptacles were comparatively dry; this introduced a difficulty, because the waxing had to be done after exposing the receptacles, and so any gametes which had collected in drops of mucilage outside the ostioles of the conceptacles were removed with the paraphyses. As far as could be judged by rough counting on the dull wax, the number of bundles of eggs thus removed was, as a rule, comparatively small. In addition to this there is the possibility that small pieces of wax may be left in the ostioles and so prevent the expulsion of gametes.

A set of exactly similar experiments was made with *Fucus serratus* (in which the paraphyses do not project from the conceptacles) as a check to the above. If the actual process of waxing has any effect on the seaweeds, it should be shown in these experiments where no paraphyses are removed by it. The results were very variable, though the mean values seem to show that, apart from the removal of the paraphyses, waxing has very little effect on the dehiscence.

The means of sixteen experiments with *Fucus spiralis* (in which waxing removes some of the paraphyses) were:—

♂ Waxed = 7 bundles liberated. Check = 13 bundles liberated
♀ Waxed = 63 „ „ Check = 166 „ „

With *Fucus serratus* (in which waxing does not remove the paraphyses) the results were:

♂ (means of 10 experiments) waxed = 16 bundles liberated.
Check = 13.
♀ (means of 4 experiments) waxed = 119 bundles liberated.
Check = 115.

The second set of experiments was carried out in London in November and December, on material which was obtained from Mersea Island, Essex. The liquid used was water, and this was selected for two reasons. First, it is not solid at ordinary temperatures, and so cannot block up the conceptacles; and, secondly, the hairs can be removed before exposing the receptacles. Two twin receptacles were put into two test-tubes; one was washed and covered with distilled water, the other similarly treated with sea-water. The test-tubes were put into larger tubes and the tops padded with cotton wool. These air jacketed tubes were put into the same freezing mixture, so that whatever effect the cold had upon the seaweeds should be shared equally by both. The distilled water froze into a solid mass; but the sea-water, owing to its higher osmotic pressure, did not freeze so readily; and when it did freeze the ice formed in crystals and not in a solid mass. It was found advisable, however, to melt any crystals when they were formed; as the mere solidification of the water round them is

No.	MALE.		FEMALE.		No.	MALE.		FEMALE.	
	Iced.	Check	Iced	Check		Iced	Check	Iced	Check
I.	4	14	102	168	VI.	5	15	34	51
II.	16	22	70	106	VII.	*9*	*9*	*54*	*48*
III.	3	7	55	81	VIII.	8	13	114	299
IV.	4	7	61	89	IX.	7	11	44	63
V.	3	5	15	31	X.	9	14	53	69

sufficient to remove some of the delicate hairs. The block of ice was broken off the one receptacle, and then both were exposed for a definite time, put into seawater, and the number of bundles of gametes expelled from each counted. The results of a series of ten experiments with *Fucus spiralis* are shown in the Table on p. 63.

The mean values are :—

♂ Iced 7 bundles expelled. Check = 12 bundles expelled.
♀ Iced = 60 ,, ,, Check = 100 ,, ,,

The values *in italics* are the only cases in which the iced receptacle does not show less dehiscence than the check. The mean values do not exhibit so large a difference as that given by the waxing method, though this may be partly due to the fact that they were made with material from a different locality, and at a different time of year. It appears, therefore, that the paraphyses play an important part in the extrusion of the gametes; the removal of some of them, and the consequent disarrangement, being sufficient to affect the mechanism considerably.

Another series of experiments was made at White Cliff Bay in which the receptacles, dried in the usual way, were allowed to extrude their reproductive bodies into fresh water instead of seawater. If the swelling of the paraphyses plays a part in the mechanism, the smaller osmotic pressure of the fresh water should cause them to swell up more and hence to expel more gametes.

No.	MALE.		FEMALE.		No.	MALE.		FEMALE.	
	F.W.	S.W.	F.W.	S.W.		F.W.	S.W.	F.W.	S.W.
I.	7	1	91	35	VII.	16	4	48	29
II.	8	3	171	92	VIII.	13	7	86	62
III.	13	6	109	73	IX.	*3*	*3*	*78*	*80*
IV.	15	6	137	99	X.	*4*	*4*	96	64
V.	16	9	138	61	XI.	3	2	*66*	*74*
VI.	19	3	92	67	XII.	2	1	54	33

As it must often rain when the plants are exposed by the tides, they must be accustomed to the action of fresh water. The values found using *Fucus spiralis* are shown in the Table. The check values with seawater were done with the twin receptacle to that used for the fresh water, as in the former experiments.

The mean values are :—

♂ F.W. = 10 bundles expelled. S.W. = 4 bundles expelled.
♀ F.W. = 97 " " S.W. = 64 " "

The values *in italics* are those in which the number in fresh water is not greater than in sea-water. The majority of these experiments were made with only a short time of exposure, for the sake of convenience.

A similar set of experiments with *Fucus serratus* gave mean values :—

♂ (means of 7 experiments) F.W.=31 bundles expelled. S.W. = 11
♀ " 2 " F.W.=113 " " S.W. = 51

Mr. E. J. Salisbury has suggested to me that the concentration of the film of sea-water covering the plants when they are exposed by the tides is an important factor in the extrusion of gametes. In view of the function of the paraphyses in this mechanism I think it is extremely probable that osmotic effects of this kind are utilized by the plant. At any rate the mechanism is by no means a simple one, and is probably made up of several factors ; among these the swelling of the paraphyses on any lowering of osmotic pressure may, I think, be reckoned.

IV.—Check Experiments by Weighing the Gametes.

As the methods employed throughout all these experiments are open to so many objections, it was thought advisable to repeat one series of experiments, using an entirely different method, as a check on the values obtained. These experiments were performed in the Laboratories at University College, London, on account of the apparatus required. The material was obtained from Mersea Island, Essex. The method employed was as follows. Fifty receptacles of *Fucus spiralis* were very carefully washed with filtered sea-water, and then dried in an oven for a definite time at 20°C (as these experiments were carried out in November and December, and the others in August, the temperature of 20°C was chosen to imitate summer conditions). They were then put into filtered sea-water. After twenty hours the receptacles were removed one by one from the liquid, washing each with distilled water into the vessel. The remaining liquid was filtered through a tared asbestos gooch crucible, with the help of a suction pump. After thorough washing with distilled water, the crucible containing the oospores was dried at 55°—60°C for some hours, cooled in a dessicator and weighed; the process of drying and weighing being repeated until the weight was constant.

The advantages of this method are:— (*a*) the use of a large number of receptacles, (*i.e.*, 50 receptacles estimated to represent about 4,200 conceptacles), and (*b*) the definite temperature used for drying the specimens, which it was not possible to obtain for the former experiments. Its disadvantages are:— (*a*) the very small weight of the gametes, which makes errors in weighing or the possible entrance of dust of considerable importance, and (*b*) the sliminess of the liquid that has contained the receptacles, which makes the whole process extremely tedious.

The results obtained are shown in the Table below. They have been compared with those found by counting the bundles of oospores (as the weight of the bundles of sperms may be considered negligeable), by working out the proportions between the results found by the two methods; and, on the whole, there is a tolerable agreement between them.

Time Dry (in hours.)	Weight in Grams.	Proportion by Weight.	Proportion by Counting.
24	0·0121	100	100
17	0·0141	118	129
6	0·0043	36	38
3	0·0034	28	40
1	0·0032	26	32
Waxed ...	0·0093	65	37
Check	0·0141	100	100
Iced	—	—	59
Freshwater ...	0·0042	125	145
Check	0·0034	100	100

The general order obtained by the two methods is the same. The weighing-waxing experiment was done at the same time, and with the same material, as the icing experiments; so it is possibly more comparable with these than with the waxing experiments done by the counting method. The results have been plotted with a dotted line on the same diagram as the values obtained by counting to show the similarity between the two curves.

V.—CONCLUSIONS.

We are now in a position to estimate, to a certain extent, some of the effects of dessication on these four species of algæ. The results have all been obtained under more or less artificial conditions; but they may serve to indicate some of the causes of the zoning observed on the shore. These effects may be briefly summarised.

Those seaweeds which grow in the upper zones are capable of resisting dessication both during germination and vegetative growth. Also their receptacles are protected by being filled with mucilage, and this seems to make their dehiscence mechanism most efficient when they are dry for a considerable length of time. Also, in both *Fucus spiralis* and *Ascophyllum nodosum* the paraphyses project considerably from the ostioles of the conceptacles; and this may be an adaptation to ensure the gametes being very rapidly expelled during the short time they are covered by water. In a few experiments with *Fucus spiralis* it was found that during the first hour, after putting a dry receptacle into water, half the number of bundles of gametes were given off that were expelled during twenty-four hours.

The seaweeds growing in the lower zones have become adapted to very rapid growth; they are thus able to supersede the more slow-growing and protected forms, in their own zones, but at the same time they have not the power of resisting dessication, so that they cannot grow in the upper zones. Also their dehiscence mechanism has become efficient for very short times of exposure; and they are able to choke out any stray member of a higher zone, growing lower down, which cannot compete with them in the number of reproductive bodies given off. At the same time in *Fucus serratus*, the lowest form, the receptacles are very little protected.

On the whole it seems as though the greatest competition had been called into play in the lowest zones, the dry and uncongenial regions of the upper shore being left to the most tolerant forms, which, if left to themselves, are able to grow anywhere on the shore.

I wish to express my warmest thanks to Professor F. W. Oliver for his kind interest and encouragement; also to Mr. A. D. Cotton for his advice and assistance, and to Miss M. K. Bohling for assistance in some of the experiments.

THE INHERITANCE OF PELORIA AND FLOWER-COLOUR IN FOXGLOVES (*DIGITALIS PURPUREA*).

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[Text-Fig. 2].

A SERIES of experiments was commenced in 1907 in order to investigate the mode of inheritance of peloria and of colour in the Foxglove (*Digitalis purpurea*). The experiments are being continued; but, owing to the biennial nature of the plant, it must be some years before they are completed. We propose therefore to publish such results as we have already obtained, to indicate the conclusions to which they point, and to supplement the present paper by another when the behaviour of the next generation of plants shall have been determined. The mode of inheritance of peloria has a special interest owing to the fact that Darwin (1868), working with the snapdragon (*Antirrhinum majus*), obtained statistics which, as Bateson (1901) has pointed out, indicate for this phenomenon a simple Mendelian mode of inheritance. Darwin's experiments (*loc. cit.*) may be summarised briefly:—

1. Peloric flowers, *selfed*, yielded plants, all peloric.

2. Peloric × non-peloric and the reciprocal cross gave F_1 all non-peloric. "I thus raised two great beds of seedlings and not one was peloric." The dominance of non-peloric over peloric was almost, but apparently not quite, complete, for "in a few instances the minute rudiment of a fifth stamen, which is always present, was more fully or even completely developed."

3. Darwin left the plants of F_I to seed themselves (without precautions against crossing) and obtained an F_2 composed of 127 plants, of which 88 were non-peloric, 2 intermediate, and 37 perfectly peloric. The experiments indicate dominance of non-peloric and precise segregation in F_2. Darwin's numbers contrasted with the numbers expected on a simple Mendelian 3 : 1 ratio are:—

Darwin's ...	non-peloric 90 ...	peloric 37
Calculated ...	non-peloric 95·25 ...	peloric 31·75

whence it is evident that the experimental results are in close agreement with those expected by Mendelian theory.

1. PELORIA IN FOXGLOVES. Turning now to our experiments with Foxgloves: all interested in gardens are aware that races of these plants are in cultivation which exhibit the phenomenon of peloria. In Foxgloves, peloria, at all events in the examples which we have had under observation, is confined to the terminal flower of the raceme. Whereas the lateral flowers retain their typical zygomorphic state, the terminal flower of a peloric plant is bell-shaped. Moreover, it stands up vertically and so forms a striking contrast with the pendulous, zygomorphic, lateral flowers. The peloric flower shows other indications of its monstrous nature; its corolla may be nine-lobed, the anthers as many as 8, and the stigma possessed of 5 stigmatic surfaces.

Though built on such abnormal and massive lines the peloric flowers of Foxgloves appear to be perfectly fertile with their own pollen. Thus the terminal, regular flowers of a peloric plant (plant B, Table I, p. 76) self-pollinated in 1907, gave seed from which 12 plants were raised. These 12 flowered in 1909 and were all peloric.

In the next place it is noteworthy that the typical, zygomorphic, lateral flowers of peloric plants carry, though they do not reveal, the factor which determines peloria. For example; the lateral flowers of a peloric plant (Plant A) selfed, gave an F_1 of 22 plants all peloric with respect to their terminal flowers. The question as to the significance of the facts just mentioned is one on which we are at present engaged; but with respect to which we are not at present prepared to make any statement. That peloria depends upon a recessive character is indicated by the following records:—

Plant D: non-peloric, selfed, 1907.
F_1=11 non-peloric and 3 peloric.

Plant E: non-peloric, selfed, 1907.
F_1=9 non-peloric and 4 peloric.

Combining the numbers obtained in these experiments we have non-peloric, 20, peloric, 7. From which we may conclude that peloria (p) is recessive to normal (P). Crosses between peloric and non-peloric confirm this conclusion. Thus plant D (non-peloric) (Pp) × plant E (non-peloric) (Pp) F_1 should give:—

1 PP : 2 Pp : 1 pp.

3 Dominant : 1 Recessive.

Our numbers=35 Dominant : 11 Recessive.

Another case: plant F (peloric) (pp) × plant E (non peloric) (Pp) should give:—

2 pp : 2 Pp.

Observed:— 16 : 24.

Peloria of Foxgloves therefore depends on a character which is recessive to normal. Inasmuch as it is characterised primarily by absence of the typical zygomorphy of normal flowers, and inasmuch as evidence is accumulating in support of the presence and absence hypothesis of the nature of dominant and recessive members of allelomorphic pairs of characters, it is not perhaps surprising to find peloria behaving as recessive to normal.

2. Flower Colour. The colour-characteristics, the mode of inheritance of which we are investigating, are white, magenta, deep magenta: red spots, brown and yellow spots, which characters are displayed by the corollas of various garden races of Foxgloves.

In Tables I and II (pp. 76, 77) are tabulated the colour-characters of the various plants under investigation and the behaviour of these characters in the F_1 generations resulting from self-fertilization of these plants, and from the cross-fertilization of plant D × plant E and plant F × plant E.

Inspection of Table I. shows that certain white plants breed true to whiteness (Plant E); others, *e.g.*, plant D, when selfed, yield an F_1 composed of white and magenta-flowered plants. Similarly when E, which, so far as the comparatively small numbers in F_1 admit of a conclusion, is to be regarded as pure to whiteness, is crossed with D, whites and magentas are obtained. We therefore conclude that Foxgloves, like *Primula sinensis* (Bateson, 1909), contain a *dominant-white* factor (W), that is a factor which inhibits the expression of colour in a zygote, the contributory gametes of which carried a colour factor. Since colour appears in F_1 from plant D selfed, that plant is not pure, but heterozygous with respect to the dominant white factor, *i.e.*, its gametic constitution is Ww. Nor may the plant D be pure with respect to magenta colour-factor (M), for, if it were, its gametic constitution would be Ww MM; it would yield gametes wM and WM and, on selfing, would produce an F_1 composed of 3 dominant white : 1 magenta, thus:—

WM.wM, male gametes.

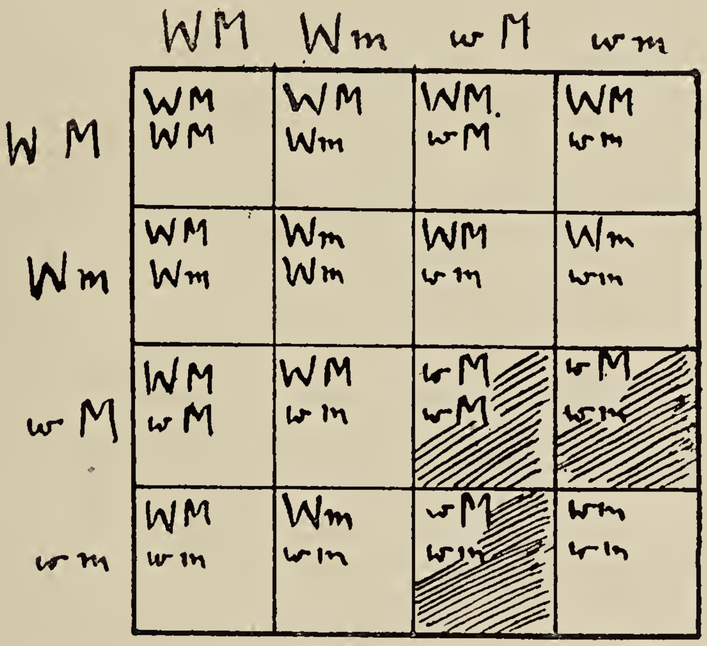
WM.wM, female ,,

giving in F_1

$$\underbrace{1\ \mathrm{WW\ MM} : 2\ \mathrm{Ww\ MM}}_{3\ \text{white}} : \underbrace{1\ \mathrm{ww\ MM}}_{1\ \text{magenta.}}$$

The result of selfing plant D,—13 white, 1 magenta,—indicates that it is heterozygous for magenta colour-factor, *i.e.*, is Mm. So that its full gametic composition with respect to ground colour is Ww Mm, and the gametes which it produces bear the characters WM, Wm, wM, wm.

Male gametes bearing these characters meeting female gametes also bearing these characters will produce zygotes, the composition of which may be indicated in the usual way (Fig. 2).



	WM	Wm	wM	wm
WM	WM WM	WM Wm	WM. wM	WM wm
Wm	WM Wm	Wm Wm	WM wm	Wm wm
wM	WM wM	WM wm	wM wM ▨	wM wm ▨
wm	WM wm	Wm wm	wM wm ▨	wm wm

Fig. 2.

Illustrating the Ratio of 13 White : 3 Magenta (shaded) in F_1 of Plant D, selfed (see Text).

Of 16 zygotes, 12 will produce white flowers because of the presence of the dominant white factor (W), 1 because of the absence of both magenta colour-factor and dominant white factor (wm). That is we shall expect a ratio of 13 white to 3 magenta. The numbers obtained in F_1 from plant D selfed are 13 whites, 1 magenta, and though it must of course be conceded that the number of F_1 plants raised is too small to provide absolute proof, yet the fairly close agreement of the numbers obtained (13 white, 1 magenta) with the numbers expected (13 white, 3 magenta) justifies the assumption that plant D is heterozygous for both the dominant-white and the magenta-colour factors.

As we shall show, the hypothesis that plant D is heterozygous for these factors permits of a reasonable interpretation of the results of other crosses.

Thus plant E, white with yellow spots, when selfed, gives an F_1 of 13 plants all white. Plant E, crossed with plant D, which contains dominant white (W), yields an F_1 containing magentas as well as whites. Therefore plant E cannot be pure with regard to the dominant white factor (WW); for, if it were, all the plants of the cross D × E would be white. It must consequently be of the constitution ww or Ww. If it is the former, it cannot, since it is white, contain the magenta colour factor M. Its complete constitution with regard to these factors must therefore be ww mm. So that D × E=Ww Mm × ww mm, and the gametes produced are of the constitution :—

Gametes of plant D:— WM, Wm, wm, wM:
Gametes of plant E :— 4 wm:

giving zygotes,

$$\underbrace{4\ \mathrm{Ww\ Mm} : 4\ \mathrm{Ww\ mm} : 4\ \mathrm{ww\ mm}}_{12\ \text{white}} : \underset{4\ \text{magenta,}}{4\ \mathrm{ww\ Mm}}$$

as compared with the actual numbers,

Obtained, 36 white : 10 magenta.
Calculated, 34·5 white : 11·5 magenta.

On the other hand, if plant E contain dominant white (W), its possible complete constitutions are :—Ww MM, Ww Mm, Ww mm.

The first two possibilities, however, are negatived by the fact that E selfed gives an F_1 all white. In the case of the third D × E=Ww Mm × Ww mm, which would produce zygotes in the ratio :—

$$\underbrace{6\ \mathrm{WM} : 6\ \mathrm{Wm} : 2\ \mathrm{wm}}_{14\ \text{white}} : \underset{2\ \text{magenta.}}{2\ \mathrm{wM}}$$

Since, however, the experimental numbers are 36 white, 10 magenta, the most probable constitution for plant E is ww mm, *i.e.*, it is recessive to both negative magenta and dominant white.

Cross F × E. Though the number (5) of plants in the F_1 of plant F selfed is too small to throw certain light on the gametic constitution of plant F, we record our attempt to determine this constitution.

Since the F_1 of the cross F × E contains magenta-flowered plants and since plant E is recessive to both magenta colour factor and dominant white factor, *i.e.*, is ww mm, plant F must contain the magenta colour factor (M). And, since plant F is itself white, if it is carrying magenta it must also be carrying the dominant white factor (W). It cannot, however, be carrying pure W, for, if it were, the cross F × E would yield an F_1 of all white-flowered plants. Therefore the gametic constitution of plant F is Ww MM or Ww Mm.

Assuming the constitution of plant F to be Ww MM, the cross F × E=Ww MM × ww mm.

The gametes produced by plant F=WM and wM, by plant E=wm, and the zygotes of F_1=1 Ww Mm : 1 ww Mm.

=1 white : 1 magenta.

On the other hand, if the second alternative be adopted, *viz.*, that plant F is heterozygous for W and M, *i.e.*, is Ww Mm, then plant F × plant E=Ww Mm × ww mm: gametes of plant F=WM, Wm, wM and wm: gametes of plant E=wm. So that F_1 will contain:—

$$\underbrace{1\text{ Ww Mm} : 1\text{ Ww mm} : 1\text{ ww mm}}_{3\text{ white}} : 1\text{ ww Mm}.$$

3 white : 1 magenta.

The numbers actually obtained, *viz.*, 15 white, 25 magenta, indicate fairly conclusively that the gametic constitution of plant F is Ww MM and *not* Ww Mm. Plant F is pure for magenta factor and heterozygous for dominant white factor.

Dark Magenta Flower Colour. Plant A, (see Table I.), bearing a deep magenta (purple) coloured flower yields an F_1 composed of 11 deep magenta (purple), 6 magenta, 5 white. If we assume the presence of a darkening factor (D) which may change magenta to purple, but which is without effect on white (*i.e.*, one which is epistatic to magenta) then a fairly close fit between expectation and realisation is obtained by ascribing to plant A a constitution of Mm Dd, *i.e.*, one heterozygous for magenta colour factor M and darkening factor D. A plant of such a constitution produces when selfed an F_1 composed of:—

$$9\text{ MD} : 3\text{ Md} : \underbrace{3\text{ mD} : 1\text{ md}}$$

9 purple : 3 magenta : 4 white,

as compared with the numbers obtained,

11 purple : 6 magenta : 5 white,

calculated on 9 : 3 : 3 : 1 ratio,

12·4 purple : 4·1 magenta : 5·5 white.

Spot Factor. Yellow, brown, or red spots occur generally in the corollas of Foxgloves. The spots vary considerably in size, contour and frequency. In white flowers the spots may be of any one of the three colours; and so far as our observations go, no Foxglove, no matter what the ground colour of the corolla may be, is altogether devoid of spots, which may, however, be so faint as to be only just distinguishable. It is not improbable that the colours, yellow and brown, of these spots are due to one and the same cause, *viz.*, the breaking down of localised groups of chromatophores: at all events yellow spots often turn brown as the flower bearing them grows older. Further, it is to be noted that, so far as we know, no flower which has a magenta ground-colour is devoid of red spots.

The distribution of red and brown spots in the F_1 generation produced by selfing plant A is noteworthy.

The numerical ratio is 17 red-spotted to 5 yellow-brown (approximately 3 : 1). The red spots, however, are confined to the flowers with magenta ground colour, the brown to the white flowers. We have ample evidence (plants D and F) that white flowers may exist with red spots. But in such cases the whites are dominant whites, and we have no evidence at present of a flower of a recessive white bearing red spots.

The behaviour of the red and yellow-brown spots appears to admit of a simple interpretation.

Reference to Table I. shows that red spots occur only in plants containing M. In the case of plant A, the presence of this magenta colour factor M is evident from inspection, since the flowers are purple. In plants D and F, however, the presence of the factor M is not directly apparent, on account of the inhibiting influence of the dominant-white factor (W), but becomes evident in the F_1 selfs and crosses. Also the plant (E), in which the factor M is absent, has yellow-brown spots. From these facts it would appear probable that the red colour of the spots is caused by the presence of the same factor (M) that is responsible for the magenta ground-colour of the corolla, and that the red spots are due to local action of magenta colour factor on the yellow-brown spot areas. If this is so, it follows that (W) the dominant white factor, which inhibits the expression of magenta ground-colour (M), is without this inhibiting effect on the M factor in the spot areas. Accepting this interpretation it follows that all white Foxgloves with red spots are dominant whites, *i.e.*, carry both W and M, also that, of white foxgloves with yellow-brown spots, all are pure recessives with respect to magenta, though some may be carrying a dominant white factor. The various theoretically possible constitutions of white Foxgloves are, therefore :—

White with red spots—WW MM, WW Mm, Ww MM, Ww Mm.
White with yellow-brown spots—ww mm, Ww mm, WW mm.

The ratios obtained by selfing and crossing which support these conclusions with respect to the nature of red and yellow-brown spots are as follows :—

Plant F (Ww MM) selfed, gives F_1, all with red spots.

Plant E (ww mm) selfed, gives F_1, all with yellow-brown spots.

Plant F × E (Ww MM × ww mm) gives F_1, all with red spots (40 plants).

Plant D (Ww Mm) selfed, gives F_1, 12 plants with red, 2 with brown spots.

Plant A (ww Mm) selfed, gives F_1, 17 plants with red, 5 with brown spots.

Totals—29 plants with red, 7 with brown spots.

Calculated—27 plants with red, 9 with brown spots.

It should be noted that in the results of plant D selfed there is a distinct departure from the expected numbers, *viz*:—

Obtained=12 : 2

Calculated=10·5 : 3·5

That this is, however, attributable to the fewness of the F_1 plants is rendered probable by the results obtained by crossing plants D and E.

Plants D × E=Ww Mm × ww mm should yield F_1 composed of 4 Mm ww : 4 Mm Ww : 4 mm Ww : 4 mm ww, that is equal numbers of red spotted and yellow-brown spotted flowers. The numbers obtained are 21 plants with red spotted, 25 with brown spotted flowers.

The hypothesis that red spots are due to magenta factor acting on yellow-brown spot-areas provides a simple explanation of the relation between colour of spots and ground colour exhibited by the F_1 from plant A; *viz.*, 17 magenta-containing plants all with red spots and 6 white plants all with yellow-brown spots. It also explains how it is that *all* the magenta Foxgloves have red spots. It is not improbable that the view which we have expressed, namely that a dominant white factor (W) is able to inhibit ground colour and not spot colour—though both ground colour and spot colour are due to the same colour factor (M),—may prove of importance in interpreting the origin of spots and bars and stripes in animals and plants. Given localised inconspicuous areas, the addition of a ground colour factor would produce a self (uniformly) coloured surface on which spots and bars and stripes might or might not stand out conspicuously. Wash over that surface with a dominant white factor and then the general ground colour will be suppressed and conspicuous splashes of colour in spots, colours or stripes will stand out on a white ground. Finally, the suggestion may be worth making, that this differential action of a dominant white factor—inhibiting ground colour but not colour in spot- or stripe-areas may provide a clue to the behaviour of such striped types (Darwin, loc. cit., p. 45, Vol. 2 and Bateson (1909), p. 99) as are known to produce, *occasionally*, self-coloured offspring.

TABLES I. AND II.

Showing inheritance of colour and marking of petals in the Foxglove (*Digitalis purpurea*).

TABLE I.—ALL PARENTS SELF-FERTILISED.

PARENTS.		F$_1$.		PROBABLE GAMETIC CONSTITUTION OF PARENTS			
Plant.	Characters.	Characters.	Number of Plants.	Peloric Factor.	Ground Colour.	Darkening Factors.	Dominant White Factors.
E	White with yellow spots	All white with yellow spots ...	13	Pp	mm	dd	ww
D	White with red spots	13 white (=11 red spots +1 brown spot +1 yellow spot) +1 magenta (=1 red spot) =12 red spots+2 brown or yellow	14	Pp	Mm	dd	Ww
F	White with red spots	4 white+1 magenta (rogue)* =5 red spots	5	pp	MM	...	Ww
A	Purple=deep magenta with red spots	5 white (=5 brown spots) +6 magenta +11 purple } (=17 red spots) =17 red spots+5 brown	22	pp	Mm	Dd	ww
B	White with purple flush and red spots	6 white (=2 red spots +2 brown spots +2 yellow spots) +5 magenta +1 magenta flush } (=6 red spots) =8 red spots+4 brown or yellow	12	pp	?	?	?

*Since all the other evidence points to peloria being recessive, this plant, which is non-peloric, is to be regarded as a rogue.

TABLE II.—CROSSES.

PARENTS.	OFFSPRING.	
	Characters.	Number of Plants.
D × E	36 white (=11 red spots +12 brown spots +13 yellow spots) +10 magenta (=10 red spots) =21 red spots + 25 brown or yellow spots	46
F × E	15 white + 25 magenta =40 red spots	40

CONCLUSIONS.

(1). Peloria in Foxgloves is a Mendelian recessive to normal.

(2). Peloric flowers and also the non-peloric flowers of peloric plants carry the recessive character.

(3). The allelomorphs responsible for colour are:—

Mm; M being magenta colour factor, dominant to m.

Dd; D being a darkening factor dominant to d and converting magenta to purple.

Ww; W being a dominant white factor in the presence of which the expression of colour due to M is inhibited so that the flowers are white.

(4). All flowers appear to be spotted. In the presence of the colour factor M, spots are red: in the absence of M they are yellow-brown. The presence of the dominant white factor W does not inhibit the expression of the colour factor M in regard to the spots (at least when present as a heterozygote=Ww).

(5). The suggestion that dominant white acts differentially on ground colour, inhibiting it generally but not in spot-areas, may prove of service in explaining the origin of bars, spots and stripes in plants and animals and also the behaviour of certain ever-sporting varieties.

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NOTES ON RECENT LITERATURE.

Professor Wille on the Classification of the Green Algæ.

"Conjugateæ und Chlorophyceæ," von N. Wille. Nachträge zu Teil. I. Abt. 2, of Engler and Prantl's *Pflanzenfamilien.*

It is now twenty years since Wille's classification of the Conjugatæ and Chlorophyceæ was published in Engler and Prantl's *Pflanzenfamilien.* During these twenty years the list of the genera included in the two groups has grown to nearly double its former size, and it is therefore not surprising that, with so many new forms to be accommodated, and with the more complete knowledge of other genera which is now at our disposal, some considerable modifications of the earlier system have been introduced. Wille, however, finds himself by no means in agreement with the "complete transformations of the system" which are characteristic of the attitude adopted in some of the more recent publications upon this subject,[1] and in his treatment of the Conjugatæ and Chlorophyceæ in the recently published Nachträge, he retains an arrangement which in respect of certain very fundamental points does not differ very greatly from that which he used in his earlier work.

Having remarked on the general agreement that a natural system must, as far as possible, be arranged phylogenetically, Wille proceeds to point out that there are two methods of constructing a system of classification ; " nach der einen stellt man zuerst doktrinär durchgreifende Merkmale auf, um die grösseren systematischen Einheiten zu trennen, und die kleineren systematischen Einheiten werden dann später, wie sie sich am besten angliedern, unter die höheren eingeordnet. Diese methode, die auch C. Linné bei seinem künstlichen Systeme verwendet wurde, ist sehr einfach und bekannt, gibt aber leider nicht ein phylogenetisches und natürliches System, sondern ein durchaus künstliches, so, wenn bei den höheren Pflanzen die Staubgefässe oder bei den Algen die Cilien als Hauptmerkmale verwendet werden."

Having coupled the system in which weight is attached to the characters of the zoospores of the Algæ with the artificial system of Linnæus, it is not surprising to find that Wille does not accept the former. But we demur strongly to the presentation of such a picture of the system, founded mainly upon the work of Klebs, Bohlin and Luther, as is suggested by this comparison. In instituting such a comparison, Wille lays himself open to the suspicion that he has lost sight of the conception underlying the formation of the groups Isokontæ, Heterokontæ, etc., in regarding only that which is actually expressed in the names chosen for them; and it is to be noticed that he speaks of the system as though it were founded, not, as it is, upon the characters of the zoospore as a whole, but upon the ciliation only.

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[1] See, for instance :—

Blackman and Tansley. "A Revision of the Classification of the Green Algæ." New Phytologist, Vol. I., 1902.

G. S. West. "British Freshwater Algæ" (especially the section entitled "Phylogeny," pp. 21-33). Cambridge University Press, 1904.

F. Oltmanns. "Morphologie und Biologie der Algen." Jena, Gustav Fischer, 1904.

The above authors give references to the literature of the more detailed work upon which the modifications introduced into the system have been mainly founded.

If the derivation of the Green Algæ from the Flagellates be accepted, as it is by Wille, surely the characters of the zoospore—the state in which the Alga presumably resembles most nearly its ancestral Flagellate type—must be of the greatest importance. Yet Wille's natural abhorrence of a system founded, as he appears to suppose, upon the single character of ciliation, leads him almost to the point of disregarding the characters of the zoospore entirely. That at least seems to be the position he takes up when he distributes forms like the Chlorothecieæ, *Mischococcus* and its allies, and *Botrydium*, among the orders of the Protococcales and reunites *Bumilleria* and *Conferva* with the Ulotrichaceæ. Yet, while taking this course, Wille admits that the Botryococcaceæ (Mischococceæ and Botryococceæ) may be derived from the Chrysomonadina, in which case they would be looked upon as forming a series parallel to the Tetrasporaceæ. Such an admission surely leaves very slender justification for including them on phylogenetic grounds with forms derivable from an ancestral type resembling the Polyblepharidaceæ.

Fully as we recognize the authority with which Wille is entitled to speak upon these matters, we feel that in this case his modifications have reduced a group hitherto consisting of organisms whose inter-relations were comparatively clear, to a state which, relatively speaking. renders it a collection of more or less heterogeneous forms.

Athough Wille's introductory remarks on the validity of the Heterokontæ are sufficiently strong, it is possible that the differences between his attitude and that of recent writers is a little over-emphasised by the arrangement he adopts, for, as we have said above, he admits the possibility of an independent origin for the Botryococcaceæ, and by doing so admits also in some degree the cogency of the arguments for the separation of the Heterokontæ from the Isokontæ. As regards the Akontæ, the name was in its origin merely the logical completion of the system of nomenclature adopted for the classes of the Green Algæ, and, with perhaps the exception of Oltmanns, who includes the Diatoms in his "Acontæ" (would that algologists could be persuaded to strive a little more effectively for some uniformity of spelling!) no one, we imagine, will be very greatly disturbed if Wille prefers the older name of Conjugatæ. Finally, the remaining group, the Stephanokontæ, is generally admitted to be very doubtfully good in the absence of any corresponding Flagellate and intermediate forms.

For the rest, we notice with pleasure that Wille deprecates the too ready granting of generic or specific rank to forms whose claims are only doubtfully established. That this tendency should continually present itself is inevitable, since the worker who is in the closest touch with any group of organisms cannot fail to be struck with the differences which exist between individuals or groups of individuals. The study of these elementary species is of great importance, but for the purposes of a general systematic work, the first essential is that a true perspective should be maintained. The union of forms which have previously borne separate names into more comprehensive genera unfortunately entails some added complications of synonomy, and no doubt opinions will differ as to the merits of the changes in particular cases.

Of the classes into which Wille divides the Chlorophyceæ, the name Chætophorales is applied to the group which corresponds generally with the old Confervoideæ, excluding, however, the Sphæropleaceæ and Cladophoraceæ, which, following later practice, are now placed with the Siphonocladiales. The class corresponds very closely with the Ulotrichales of Blackman and Tansley and of Oltmanns, and it was perhaps unnecessary to invent a new name, more especially as the divergence is much less than that which exists between the new Protococcales (Wille) and the groups of the same name of Blackman and Tansley and of Oltmanns. Following recent practice, the old Siphoneæ have been divided into two groups, the Siphonales and Siphonocladiales.

As regards the nomenclature of the orders, the new orders Botryococcaceæ and Ophiocytiaceæ necessarily follow from Wille's views with regard to the Heterokontæ, and perhaps the same applies to the order Hydrogastraceæ, which is formed to receive *Botrydium* and *Protosiphon*, since the older name of Botrydiaceæ has in recent years been restricted to the Heterokontous forms. In the Chætophorales, the formation of the independent order Aphanochætaceæ is the only logical alternative to the inclusion of Aphanochæte and Coleochæte (Coleochætaceæ) with the Chætophoraceæ. The three genera *Trentepohlia*, *Phycopeltis* and *Cephaleuros* form a very natural and strongly characterized group and we are glad to see that Wille agrees with Oltmanns in giving them rank as the order Chroolepidaceæ.

The general form of the *Pflanzenfamilien* is so familiar that no further comment is needed, and though we disagree with the author's views as to the value of the characters of the zoospore from a systematic point of view, we are none the less highly appreciative of the care and thought which has been devoted to the revision of this section.

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THE INTER-RELATIONSHIPS OF THE BRYOPHYTA

BY F. CAVERS, D.SC.

INTRODUCTION.

IN the present series of articles the writer proposes to give a summary and discussion of the morphology and affinities of the Bryophyta, together with lists of literature, which it is hoped may be of use to students interested in the group. For details and figures, since no attempt at completeness will be made here, reference should be made to the well-known works of Campbell ("Mosses and Ferns"), Goebel ("Organography of Plants"), and Lotsy ("Vorträge über botanische Stammesgeschichte," Band 2).

With some exceptions, the classification adopted in the "Pflanzenfamilien" of Engler and Prantl will be followed. The commonly accepted division of the Bryophyta into Hepaticæ (Liverworts) and Musci (Mosses) has, however, been challenged by several recent writers. The anomalous position of the Anthocerotales among the Hepaticæ was recognized by Leitgeb in his classical work ("Untersuchungen über die Lebermoose"). Gayet, in a paper on the development of the Bryophyte archegonium (which will be referred to later), definitely proposed to raise this family to the rank of a class co-ordinate with the Hepaticæ and the Musci, and Howe (18) first defined this class and named it the Anthocerotes. The propriety of this three-fold division of the Bryophyta will be discussed when the Anthocerotales are dealt with.

I.—SPHÆROCARPALES.

Setting aside the Anthocerotales, or Anthocerotes, for the present, the Hepaticæ have generally been divided into Marchantiales and Jungermanniales. In the Marchantiales the plant-body is invariably a thallus of simple external form. The growing-point consists of a group of initial cells; when apical branching is about to occur, the group broadens out, the middle region grows forward and its cells stop dividing, and we get two growing-points separated by a "middle lobe." The apical branching is usually "dichotomous," owing to equal or sub-equal growth of the two new growing-points. Apart from the erect gametophores of the higher forms, the branches of the thallus grow solely in the horizontal plane, whether they are formed by "dichotomy" of the growing-point or arise laterally from the underside of the "midrib," and the margins are entire. Throughout the group, however, the thallus tissue is differentiated (except in the genera *Monoclea* and *Dumortiera*) into an upper zone of green tissue with air-chambers, opening by pores on the surface, and a lower zone of compact colourless tissue which serves for food-storage, frequently contains fungal hyphae, and is sometimes traversed by sclerotic fibres or by mucilage ducts. The lower surface bears scales and two kinds of rhizoids; of these some spring from the bases and the axils of the scales (which are typically arranged in two longitudinal rows), are provided with short peglike internal thickenings of the cell-wall (tuberculate rhizoids), and run back parallel with the underside of the thallus, while the others have smooth walls, have no relation to the scales, and grow directly downwards into the substratum. The sexual organs are either scattered over the thallus and separately embedded in it, or are collected into groups (receptacles) which are either sessile or stalked. The antheridium consists at an early stage of a row of cells, owing to repeated transverse divisions taking place in the mother-cell anterior to the formation of the first vertical walls. The archegonium neck consists of six rows of cells. The embryo sporophyte typically shows an octant stage; the mature capsule has (except in *Monoclea*) either no seta or a very short one; the capsule wall consists of a single layer of cells, and it opens in various ways but probably never splits into four equal valves. The spore mother-cell does not (except in *Targionia* and *Monoclea*) become four-lobed.

In the Jungermanniales, the plant-body is, in the vast majority of cases, differentiated into a cylindrical stem and two or three rows of leaves (one cell in thickness, with rare exceptions). When it is thalloid, it never has air chambers, but it shows a great variety of form and mode of branching, with a strong tendency to the formation of simple or branched lobes or leaves. Apical growth is always effected by a single apical cell; in the leafy forms this cell is generally a three-sided pyramid, in the thalloid forms it varies in shape. In apical branching, the apical cell of the branch is constituted of a segment cut from the parent apical cell, and the branching is typically monopodial. There are no tuberculate rhizoids. The sexual organs are usually developed in groups, but never on special stalked receptacles. In the young antheridium vertical divisions set in at a very early stage, usually after a single transverse division of the mother-cell. The neck of the archegonium consists of five rows of cells. The embryo typically divides by repeated transverse walls, the lower (hypobasal) of the two cells formed by the first division usually taking no further part in the development of the sporophyte; there is no octant stage. The sporogonium usually has a relatively long seta, and the capsule nearly always opens by four valves, never by a lid. The spore mother-cell becomes deeply four-lobed before the tetrad division occurs.

Though these two groups are, on the whole, sharply distinguished, there are interesting cross-affinities between the lowest members of the two groups. The Ricciaceæ, the lowest of the Marchantiales, present the simplest type of sporophyte, in which sterilisation is (except in *Tessellina*) confined to a single peripheral layer of cells, forming an epidermis or capsule-wall around the wholly sporogenous central tissue. In this respect the Ricciaceæ are sharply marked off from all other Bryophytes, but in the structure of the thallus and of the sexual organs they agree closely with the higher Marchantiales.

The small families Sphærocarpoideæ and Rielloideæ, which Schiffner (27) places at the base of the Jungermanniales, are regarded by Goebel and by Lotsy as belonging to the Marchantiales, and as a matter of fact they were included in the Ricciaceæ by the earlier systematists. These two families agree with the Jungermanniales in having no air-chambers in the thallus, in having no tuberculate rhizoids, and in showing a marked tendency towards the development of leaves; but they agree with the Marchantiales in the development of the sexual organs, in the early stages of embryogeny, and in having a single-layered capsule wall. Finally, they show certain peculiarities not found elsewhere in the Liverworts—the special envelope around each antheridium and archegonium in both families, and the curious wing of *Riella*. It would seem advisable, if these families must be removed from the Jungermanniales, to place them in a special group—for which the name *Sphærocarpales* is suggested—quite independent of the Marchantiales and the Jungermanniales, though showing affinities with both of these groups.

Were we to take the further step of transferring the Ricciaceæ from the Marchantiales and uniting them with the Sphærocarpales, we should have a synthetic generalised group which would practically realise our conception of the common ancestral stock from which were probably derived the Marchantiales and the Jungermanniales. But the affinities of the Ricciaceæ with the higher Marchantiales are so close, especially when we take into account the transitional group Corsiniaceæ, that such a step hardly seems justifiable. However, starting from a hypothetical ancestral form (Lotsy's " Sphæro-riccia ") with the simple type of thallus found in *Sphærocarpus* (but without the envelopes of the sexual organs) and the simple sporophyte of a *Riccia*, the evolution of the Hepaticæ (excluding the Anthocerotales) may readily be regarded as having proceeded along two diverging lines. The *Marchantia* line is marked by elaboration in the internal structure of the thallus and by the aggregation of the sexual organs into receptacles of increasing complexity; while the *Jungermannia* line shows external differentiation of the plant-body, leading to the typical leafy Acrogynæ, the internal structure of the vegetative organs remaining in most cases simple, though the capsule attains greater specialisation in internal structure than in the Marchantiales.

SPHÆROCARPACEÆ.

The Sphærocarpales may be divided into two orders—the Sphærocarpaceæ with two genera (*Sphærocarpus*, *Geothallus*) and the Riellaceæ with the single genus *Riella*.

The most striking features of the Sphærocarpales are the presence of a special envelope around each antheridium and archegonium ; the absence of typical elaters, which are represented only by sterile archesporial cells mixed with the spores ; the feeble development of the sporogonial seta ; and the absence of fibrous thickenings from the single-layered capsule wall, which merely decays to set the spores free.

Most species of *Sphærocarpus* have a very simple thallus, with notched margins, each notch marking the position of a growing point with an apical cell from which segments are cut off above and below, as well as laterally. The thallus consists almost entirely of uniform green cells, arranged in several layers at the middle, where it is attached to the soil by rhizoids, and thinning out to a single layer at the margins. At the growing points, there are, especially on the underside, mucilage-hairs consisting of a row of cells, the terminal cell being large and club-shaped. Petounnikow (25), who, in 1867, discovered the male plants of *Sphærocarpus*, regarded these hairs as rudimentary leaves, corresponding to the

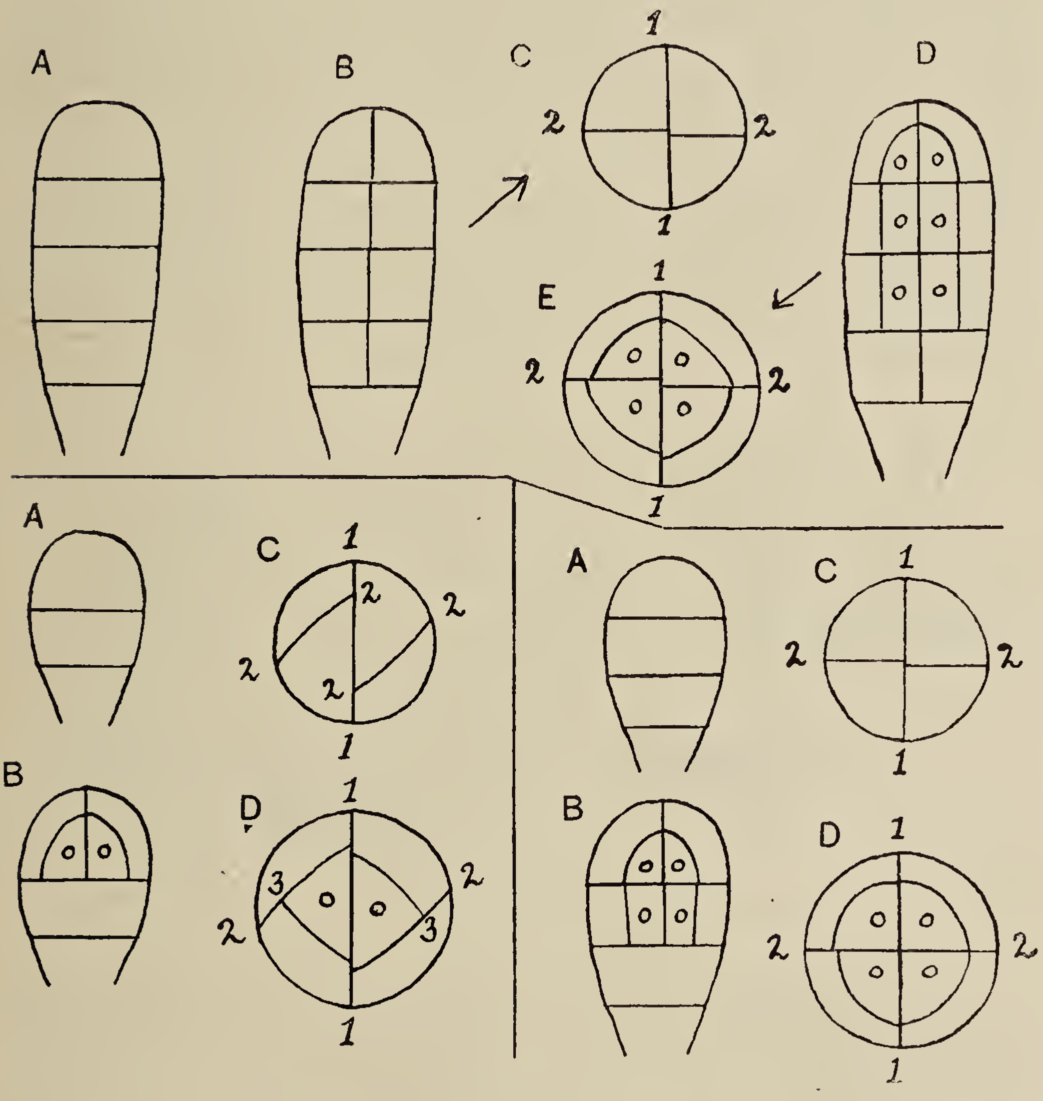

Fig. 1. Diagrams illustrating the early development of the Antheridium in Marchantiales (upper row), Sphærocarpales (lower row, right), and Jungermanniales (lower row, left); cross-sections shown in C and E of upper series, and in C and D of lower series.

ventral scales of the Marchantiales and the amphigastria or under-leaves of the Acrogynæ, and there is abundant evidence for the view that leaves have arisen, in various groups of Liverworts, from mucilage-hairs primarily adapted for protection of the growing apex. Campbell (4) discovered in plants of *S. californicus*, growing in unusually moist and shaded places, regular marginal lobes or leaves comparable with those of *Blasia* or *Fossombronia*.

The genus is diœcious, the male plants being extremely small, (usually little more than 0·1 mm. in diameter) and often covered by the larger female plants. The development of the antheridium is interesting, since it forms a type intermediate between those observed in the Marchantiales and the Jungermanniales (Fig. 1.) The mother-cell divides transversely; the basal cell undergoes no further division, but the upper divides to form three superposed cells; of these the lowest divides again to form the short stalk, while vertical walls appear in the two upper cells, giving an octant stage. In each of the eight cells a periclinal wall is then formed, cutting off a wall-cell from a primary sperm-cell. The body of the ripe antheridium is spherical. The surrounding cells of the thallus grow out to form an envelope which extends far beyond the antheridium itself and becomes flask-shaped (Fig. 2,A).

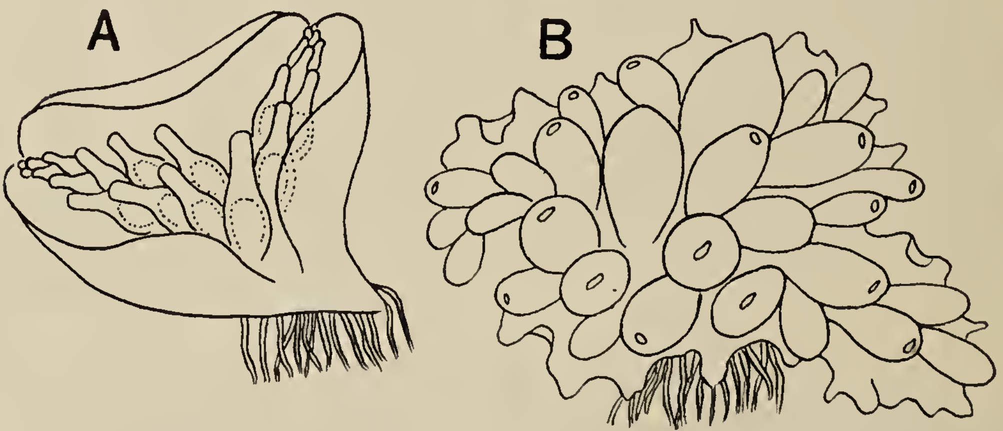

Fig. 2. *Sphærocarpus terrestris*. A, a male plant, × 40; B, a female plant, × 10.

The archegonium shows the typical Liverwort development, fully described by Campbell (3). When mature, it is sessile, and its neck consists of six rows of cells, with an axial row of four canal cells; it should be noted that the archegonium of the Sphærocarpales exactly resembles that of the Marchantiales, whereas in Jungermanniales there is usually a stalk and there are five rows of neck-cells. The neck is strongly curved forwards, as is the envelope which grows up around the archegonium (Fig. 2, B). The envelope develops independently of fertilisation, and loosely invests the archegonium; like that of the antheridium, it consists of a single layer of cells.

The embryogeny is of the Marchantiales type, the first (basal) wall being transverse, and the lower cell giving rise to the foot of the sporogonium, which is separated from the spherical capsule by a short neck-like seta. The archesporial cells at first contain chloroplasts and starch-grains, but after a time these are replaced by oil-drops in certain cells, and these cells give rise to the spores. The spore mother-cells are spherical and do not become lobed before the tetrad division; in this respect *Sphærocarpus* differs from the Jungermanniales and resembles the Marchantiales. The sterile cells retain their starch, and according to Leclerc du Sablon (21) they resemble the spore mother-cells in the division of the nucleus into four; they become ovoid in form and are used up by the developing spores. The calyptra, formed from the venter of the archegonium, is ruptured by the increase in volume of the ripening capsule, and the spores are set free by the decay of the capsule wall and of the envelope. In *S. terrestris* the four spores of the tetrad remain united within a common outer spore-coat, and as has been shown by Douin (11) and by Strasburger (32), of the four resulting plants, two are commonly male and two female. In *S. Donnellii*, however, the four spores separate when mature, and in *S. cristatus* the spores separate long before the capsule ripens.

Geothallus, discovered and described by Campbell (5, 6), is a Californian genus closely allied to *Sphærocarpus*, from which it differs in being a much larger plant and in the definite organisation of leaves. Moreover, the plant is perennial, and at the beginning of the dry season the younger part of the axis is converted into a tuber in which food is stored up, the apex persisting and resuming growth with the return of favourable conditions. The sexual organs and sporogonium are very similar to those of *Sphærocarpus*, and the chief interest of the genus centres in the differentiation of the plant body into axis and leaves. A leaf is formed from each lateral segment cut from the apical cell. The leaves are at first placed vertically, but later become shifted so as to be "succubous" (*i.e.*, the hinder edge of each leaf overlaps the anterior edge of the leaf behind it) or horizontal. This marks a great advance upon *Sphærocarpus*, in which the leaves are simply wings of the thallus interrupted by the notches in which the growing-points are situated. In *Geothallus*, leaf-like outgrowths also arise from the upper surface of the axis, and sometimes these are continuous with the lateral leaves. A similar arrangement occurs in the genus *Petalophyllum*, and this, together with the tuber formation which occurs in both genera, led Goebel (13) to the view that *Geothallus* is closely allied to *Petalophyllum*; but we meet with the same thing again in a species of *Anthoceros*, and it is obviously nothing more than a case of homoplasy—which, as has been pointed out by Farmer and by Goebel, the Hepaticæ show to an extent that cannot be paralleled by any other group of plants.

RIELLACEÆ.

Until 1902 the remarkable aquatic genus *Riella* was supposed to be confined to the Mediterranean basin, the seven species then known having been recorded from Algeria, France, Sardinia, and the Lake of Geneva (*R. Reuteri*, described by Hofmeister, but long ago destroyed owing to the erection of a mill on the lake-side). New species have since been described from Turkestan by Porsild (26), from Texas and the Grand Canary by Howe and Underwood (19), and from Port Elizabeth, South Africa, by the writer (7)—*R. capensis* is of interest as extending the range of the genus to the Southern Hemisphere. A paper on *R. capensis*, and on the genus generally, is being prepared for publication.

Riella closely resembles *Sphærocarpus* and *Geothallus* in the structure of the sexual organs and sporophyte, but differs greatly from these genera in having a cylindrical axis or stem which is produced dorsally into a wing-like expansion, besides bearing a row of leaves on either side at the base of the wing. In *R. bialata*, recently described by Trabut (37), there are two wings, right and left, both arising from the dorsal side of the stem.

The morphology of *Riella* has been much discussed. Several writers have doubted the accuracy of Montagne's original description and figure (1, 2) of *R. helicophylla*, the first species to be discovered, in which the wing was represented as being wound in a close spiral, like the thread of a screw, around the erect stem. Leitgeb (22) confirmed this description, found that the cells of the axis showed spiral twisting, and suggested that the wing arose at a late stage, after the stem had coiled around some supporting water-plant; this suggestion of a climbing habit was quite erroneous, but Leitgeb had only herbarium material. Later writers supposed that the spiral appearance of the wing was simply an optical illusion, and that the wing was merely folded and wavy, as is certainly the case in *R. capensis* (Fig. 3). Quite recently, however, *R. helicophylla* has

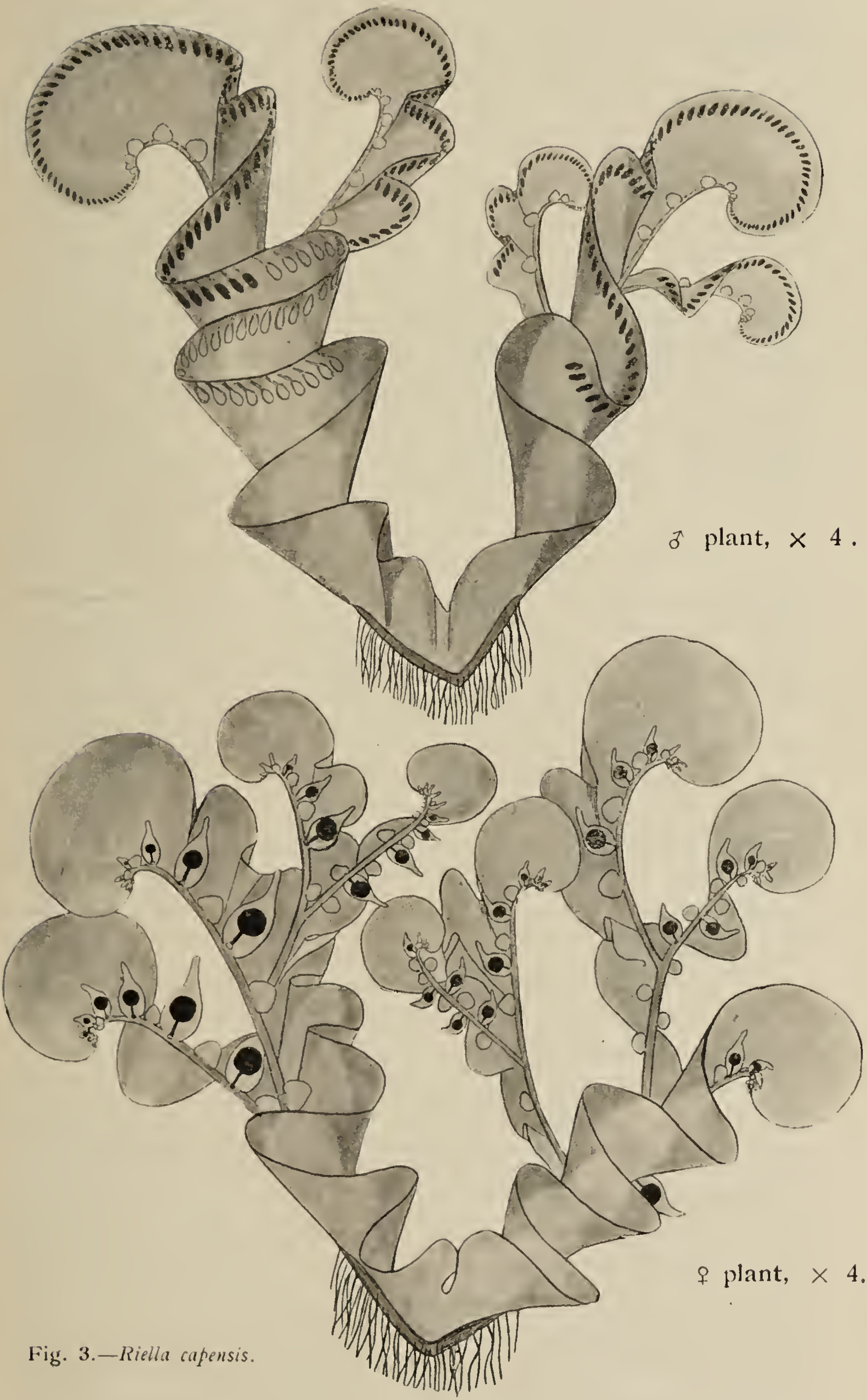
♂ plant, × 4.
♀ plant, × 4.

Fig. 3.—*Riella capensis.*

been again examined by Porsild (26) and by Müller (24), and it would appear that Montagne's account of this species was quite correct.

The nature of the wing itself has formed the subject of conflicting statements. Hofmeister (17) compared the *Riella* plant to a *Marchantia* or a *Metzgeria* in which the thin lateral wing had developed only on one side of the midrib, and Goebel has recently adopted this explanation in a somewhat modified form, basing his interpretation chiefly on observations made with young plants. Goebel's "Profilstellung" theory of the organisation of *Riella* assumes that this genus differs from all other Liverworts in that the development of the thallus is in the vertical instead of in the horizontal plane; that the whole tissue of the young plant arising from the spore is at first meristematic and consists of a single layer of cells; that later an intercalary growing-point arises either at one place or at two opposite places on the margin of the plate; that the new cells formed on the upper or distal side of the growing-point then contribute to the growth of the one-layered wing, while those formed on the lower or proximal side go to form the cylindrical stem. Solms (30), however, upholds Leitgeb's view that the plant is dorsiventral and that the wing is simply a dorsal outgrowth; and it is difficult to see how Goebel's explanation could be applied to the case of *R. bialata*. The extreme plasticity of the Hepatic plant-body renders elaborate interpretations of the "Profilstellung" kind quite unnecessary, just as this plasticity completely baffles the attempt sometimes made to distinguish between "thallus-lobes" and "leaves" in this group. Schiffner (29) has described and figured the occurrence of leaf-like organs on the marginal portion of the wing in *R. Battandieri*.

A comparison of the descriptions and figures in the literature of the genus, and the examination of specimens of most of the species hitherto discovered, shows that there is on the whole a definite correlation between the breadth of the wing and the size of the leaves; the broader the wing, the smaller are the leaves, and *vice versâ*. The form of the plant depends very largely upon the external conditions of growth, especially the depth at which it grows in the water and the light which falls upon it. Most of the species grow erect in fairly deep water, and have a broad wing, usually thrown into folds, and relatively small leaves; these erect species are attached to the mud by rhizoids at the base of the stem. Some species, growing in shallow water, have a creeping stem, attached along its whole length by rhizoids; here the leaves are relatively large and the wing narrow. The same is the case in *R. Clausonis*, which has unusually large leaves, while the narrow wing remains undeveloped in places, and rhizoids are absent; this species frequently floats on the surface of ponds. Corbière (8) observed that plants of *R. gallica* which had been stranded on mud, owing to the drying of the pond, were attached by means of rhizoids given off all along the stem; he regards this plant as merely a variety of *R. Battandieri*, which grows erect in water.

The antheridia are produced on the free edge of the wing and become enclosed separately in pockets formed by local thickening of the otherwise one-layered wing. The archegonia, each surrounded by a flask-like envelope, which is smooth in some species, but in others has eight longitudinal folds, are developed on the stem at the base of the wing; some species are diœcious, others monœcious.

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II.—MARCHANTIALES.

This group, as already defined, is divided by Schiffner, Müller, and other systematists, into two orders, Ricciaceæ and Marchantiaceæ.

In the Ricciaceæ, which includes the two genera *Riccia* and *Tessellina*, the green upper zone of the thallus consists either of erect filaments separated by narrow air-spaces, or of a network of lamellæ which are generally roofed over to form wide chambers; in the latter case, however, the chambers are devoid of special assimilating outgrowths. The air-pores are surrounded by a single ring of cells. Ventral scales are generally present, but are often small, and never show differentiation of an appendage. The sexual organs are developed singly and each becomes deeply embedded in the thallus; the canal of the antheridial cavity is often prolonged into a conical or cylindrical ostiole, and the archegonium neck is generally exserted from the archegonial cavity. The sporophyte is a simple spore-fruit or capsule, without seta or foot; sterilisation is limited to the production of a single-layered wall. The capsule remains enclosed in the calyptra, and the spores escape by decay of the capsule wall, the calyptra, and the surrounding tissue of the thallus.

In the Marchantiaceæ, the green zone of the thallus consists of well-developed air-chambers (except in *Dumortiera* and *Monoclea*), which generally either contain loose filamentous assimilating tissue or are divided into secondary chambers by chlorophyll-bearing lamellæ. The air-pores are surrounded by a single ring, or by several concentric rings, or by several superposed rings, of modified epidermal cells. The sexual organs are nearly always aggregated into receptacles, or gametophores; in all except the lowest forms the archegoniophores are stalked, as are also the antheridiophores in the highest forms. The sporophyte is differentiated into foot, seta, and capsule, and the latter is when ripe pushed through the calyptra; except in *Corsinia* the sterile inner cells of the capsule are developed as elaters with fibrous thickenings.

Since the publication of Schiffner's classification of the Marchantiales, considerable additions have been made to our knowledge of the group, and on various grounds it seems necessary to propose certain modifications in Schiffner's scheme. Schiffner divides the Marchantiaceæ into three sub-orders—Corsinioideæ, Targionioideæ, and Marchantioideæ. These, it is now suggested, should be raised to the rank of orders. There is no sharp distinction between the Ricciaceæ and Schiffner's Marchantiaceæ, except in the structure of the sporophyte, and even in this respect *Tessellina* shows an approach to a connecting link between the two groups. At any rate, it seems hardly justifiable to set the Ricciaceæ against the whole of the remaining Marchantiales. The genus *Monoclea*, which must now be removed from the Jungermanniales, should in the writer's opinion be placed in an order (Monocleaceæ) by itself, standing between the Corsiniaceæ and the Targioniaceæ. With the Marchantiaceæ in the restricted sense (corresponding to Schiffner's Marchantioideæ), we thus get five orders of Marchantiales.

RICCIACEÆ.

In most species of *Riccia* the upper zone of the thallus consists of narrow vertical air-canals, each bounded by four of the filaments produced by outgrowth and repeated transverse division of a superficial cell. The terminal cell of each filament is usually larger than the rest, forming with the corresponding cells of the neighbouring filaments a sort of epidermis of hyaline cells containing few or no chloroplasts (Fig. 4). In many species, each of these epidermal cells becomes divided into an upper and a lower cell, and the former eventually dries up and collapses, leaving only the lower part of its

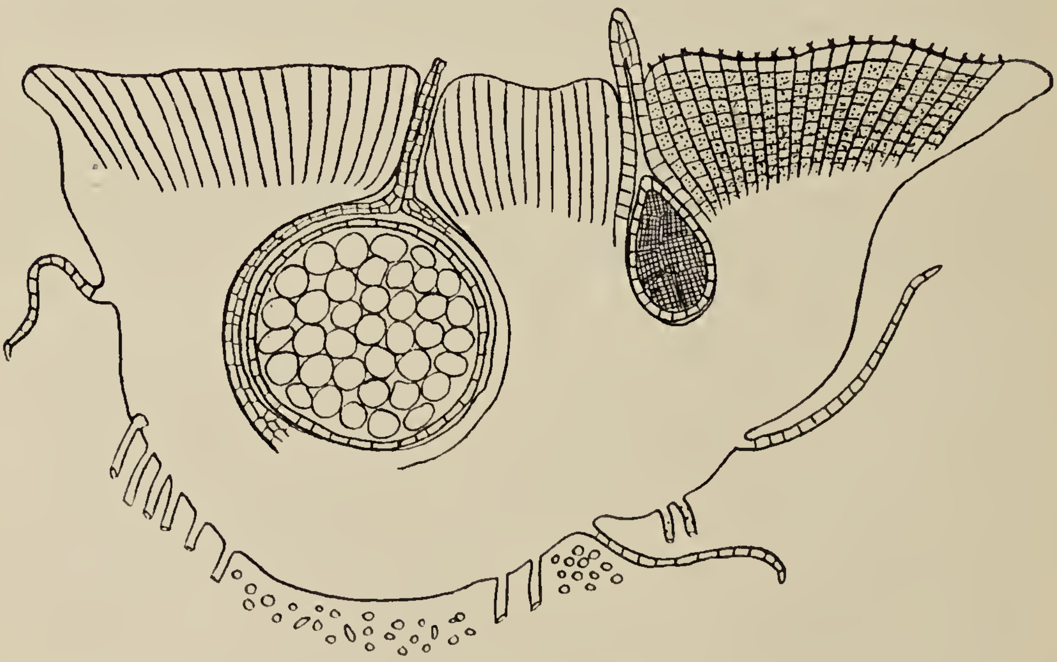

Fig. 4. *Riccia glaucescens*. Transverse section of thallus with an unripe sporogonium on the left and an antheridium on the right.

wall as a cup. Sometimes each epidermal cell grows out into a long colourless hair.

In several species the air-canals become drawn out into wide chambers, bounded by cell-plates; these species have by different writers been separated under the name *Ricciella*, regarded by some as a sub-genus of *Riccia* and by others as an independent genus. In *R. crystallina*, which grows in very moist and shaded places, the wide chambers remain open above and form shallow cavities separated by a network of thin vertical partitions. In *R. fluitans*, the chambers are roofed over by a layer of cells; in sterile aquatic plants, which float just under the surface-film of the water, the chambers are closed, but in the land form a pore is left in the roof of each chamber. In some allied species, the chambers are partitioned up, so as to form two or more superposed tiers as seen in cross-section of the thallus. The figure given in various text-books as the land-form of *R. fluitans*, e.g., in Fig. 379 of the English edition of Strasburger's "Text-book of Botany," is in reality a representation of *R. natans*; the land form of *R. fluitans* differs from the water-form only in having rhizoids, sexual organs and fruits, but not in the general habit of the thallus.

Riccia natans is also an amphibious species, and it too has been separated as a distinct genus, *Ricciocarpus*, but the recent investigation of this plant by Lewis (14) and by Garber (8) has shown

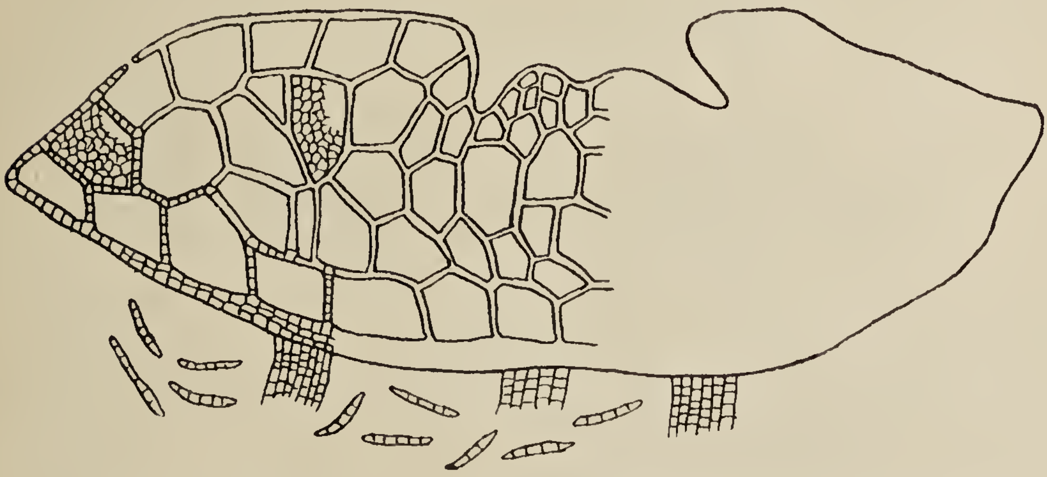

Fig. 5. *Riccia natans.* Transverse section of thallus showing air-chambers and ventral scales.

conclusively that the older systematists were correct in including it in the genus *Riccia*. The sterile free-floating aquatic form has a broad thallus, and the air-chambers are divided up by plates of tissue, so that the thallus comes to consist almost entirely of a spongy mass, the compact ventral tissue being reduced to two or three layers of cells (Fig. 5). The ventral scales are long and narrow and are scattered over the whole underside of the thallus; they shew long-continued growth in length owing to the basal cells being meristematic. In the land-form, which Lindberg (Bot. Centralblatt, Band 6, p. 363) showed to be identical with *Riccia lutescens* (a fact recently discovered independently by Lewis), the thallus is of simpler structure and the scales are short and semilunar in shape. In the other species of *Riccia*, the scales are developed in a single series, but they usually become split in the middle, giving rise to two lateral rows; in the hygrophilous species they soon perish, but in xerophilous species they are large and persistent.

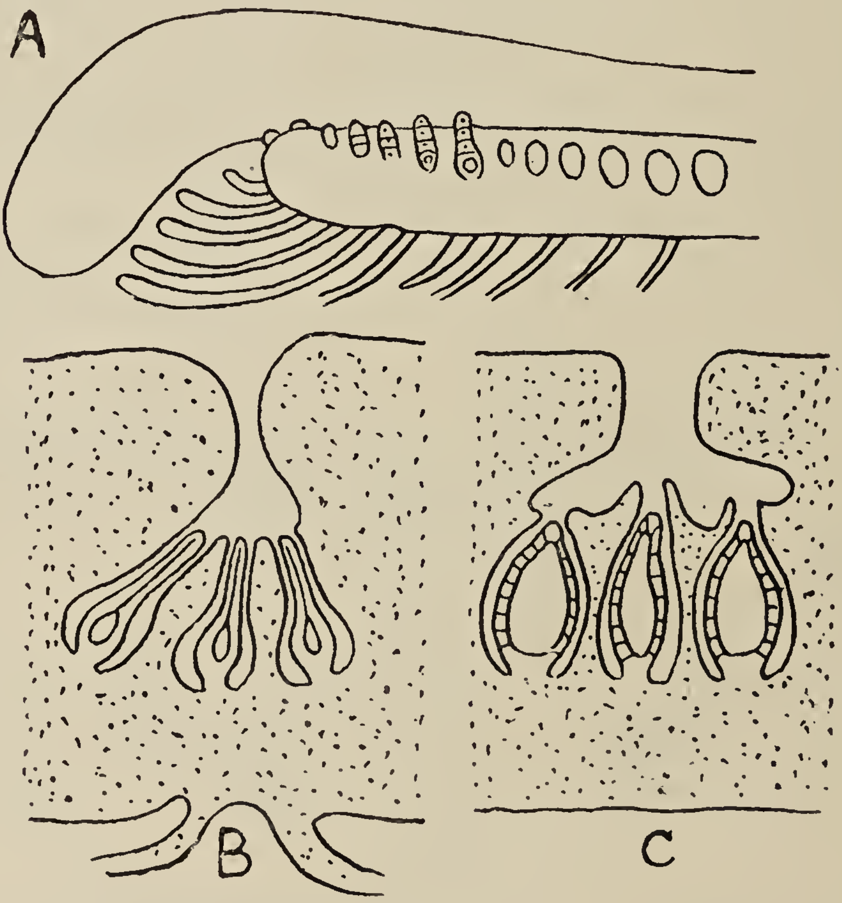

Fig. 6. *Riccia natans.* A, longitudinal section of thallus, showing antheridia and archegonia; B. transverse section of archegonium-bearing portion; C, transverse section of antheridium-bearing portion. After Garber.

The sexual organs are usually scattered, and sunk separately in deep cavities. In some species there is a tendency to the aggregation of the antheridia into groups, and this is very pronounced in *R. natans*, in which these organs are developed in two or three rows on a long receptacle, forming a ridge with a groove on either side and arched over by the neighbouring tissue of the thallus (Fig. 6).

In *Tessellina* (Fig. 7), the air-chambers are arranged in a single series, and each opens by a pore which is raised above the surface of the thallus and surrounded by five or six cells with strongly thickened radial walls. The ventral scales arise in two independent rows, as in the higher Marchantiales. The antheridia are in groups, marked by tufts of hairs among which arise the cylindrical ostioles of the antheridial chambers. In the female plant, each archegonium becomes surrounded by a conspicuous green conical outgrowth containing air-chambers. As was shown by Leitgeb, the capsule contains rounded sterile cells, but since these lie just within the capsule-wall, it is doubtful whether they can be regarded as sterile archesporial cells. Leitgeb[1] thought these sterile cells represented

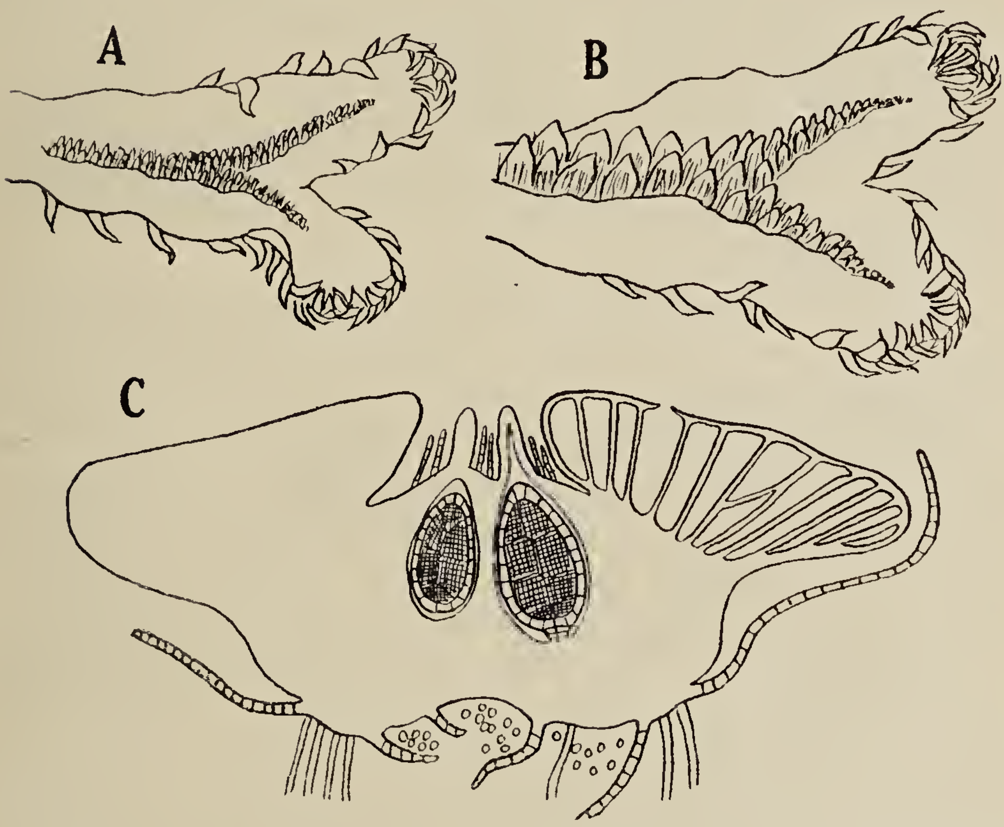

Fig. 7. *Tesselina pyramidata.* A, a male plant, × 2 ; B, a female plant, × 2 ; C, transverse section of a male plant, showing two antheridia.

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[1] Untersuchungen, IV., p. 45.

a rudimentary doubling of the normally single-layered wall of the fruit, but throughout the Marchantiales the capsule-wall consists of a single layer of cells, except for the apical thickened cap frequently found in the higher families. Hence the interpretation of these sterile cells in *Tessellina* remains an open question.

CORSINIACEÆ.

In the two genera belonging here, the archegonia are developed in sunken groups on the upper side of the thallus, each group being protected by the outgrowth of the thallus-tissue; the capsule is separated from the foot by a short neck-like seta, and its wall becomes disorganised to set the spores free. The air-chambers are arranged in a single layer, and each chamber opens by a pore surrounded by a single ring of cells.

In *Corsinia* the cells forming the floor of the chambers generally grow out to form short assimilating filaments, but sometimes these are wanting. The ventral scales are small and are scattered over the whole underside of the thallus, as in *Riccia natans*; each scale has on its free margin a long threadlike appendage, and at the front of the thallus these appendages bend up over the growing-point, in the same way as the more highly developed appendages characteristic of the ventral scales of the higher orders of Marchantiales.

The antheridia are collected into a receptacle which has the form of a ridge, as in *Riccia natans*; sometimes it is forked in front owing to branching of the apex, but the growing-point of the thallus is not used up in the development of the receptacle, hence several receptacles may be formed one after another. Each archegonial group, containing from six to ten archegonia, accompanied by numerous hairs (paraphyses) lies in a depression of the thallus; several groups may be formed in succession, the growing apex not being used up. The developing sporogonium is protected by a curious involucre, which grows up from the depression and becomes lobed, the lobes containing air-chambers (Fig. 8). This outgrowth is not fully formed unless fertilisation occurs; if only one archegonium develops a fruit, the involucre bends over it and shows one-sided growth, becoming palmately lobed, but if several fruits are formed, the outgrowth becomes radially symmetrical and peltate, its lobes covering the developing fruits. The capsule contains numerous sterile cells mixed with the spore mother-cells, but neither these cells nor those forming the capsule-wall bear fibrous thickenings (Fig. 9).

Corsinia, though showing distinct affinities with the Ricciaceæ, makes some important advances upon that family, especially in the more definite organisation of the receptacles, or gametophores, and in the structure of the sporophyte, as well as in that of the thallus. The curious outgrowth which arises in the midst of the archegonia (Fig. 8) foreshadows the elaborate archegoniophore, or carpocephalum, of the higher Marchantiales.

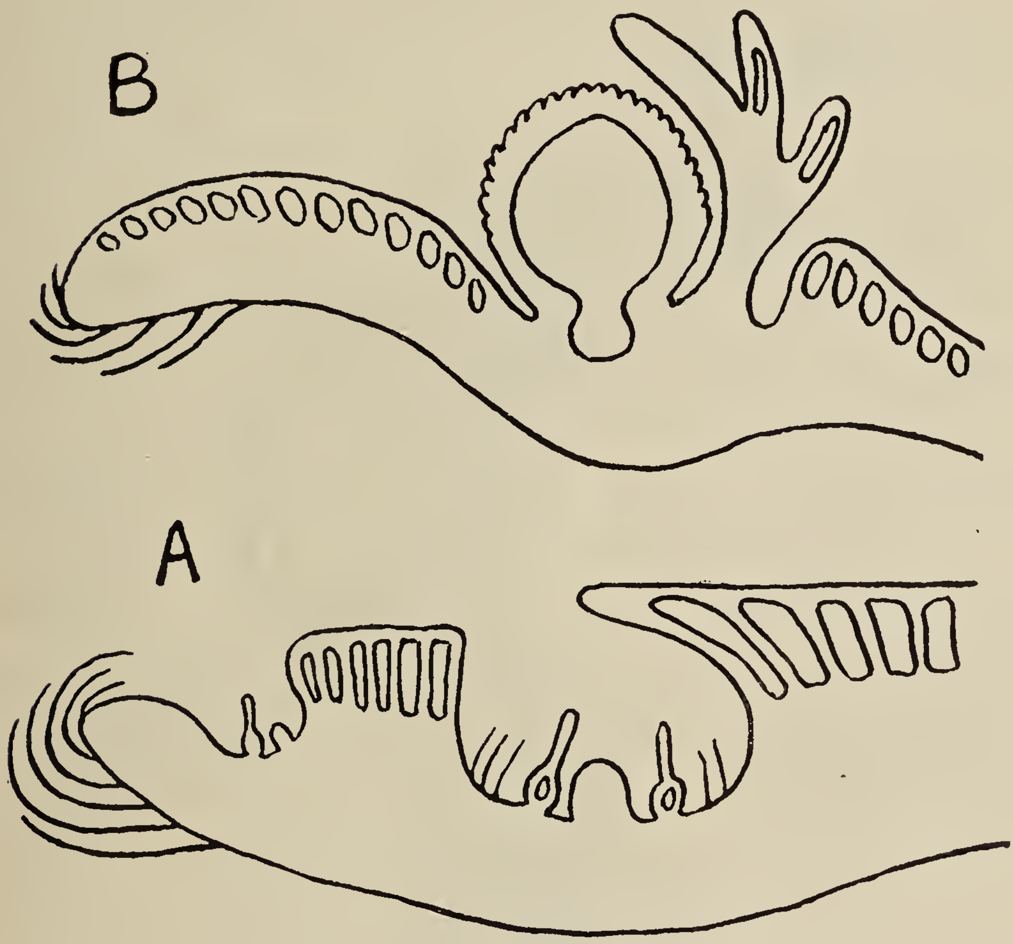


Fig. 8. *Corsinia marchantioides*. Longitudinal sections of thallus. A, shows the outgrowth arising in the midst of the archegonial group ; B, a later stage, with a young sporogonium. After Leitgeb.

Boschia, with a single species, is found only in Brazil ; our knowledge of this interesting plant is due to Leitgeb.[1] It has the habit of a xerophilous *Riccia*. The large two-rowed ventral scales roll up over the narrow thallus in the dry state ; the air-chambers contain well-developed filaments. The antheridia are developed in a row on the midrib of the male plant, but are not collected into a definite antheridiophore. The archegonia are produced in groups

[1] Unters, iv., p. 57.

of three or four, each group sunk in a cup-like depression

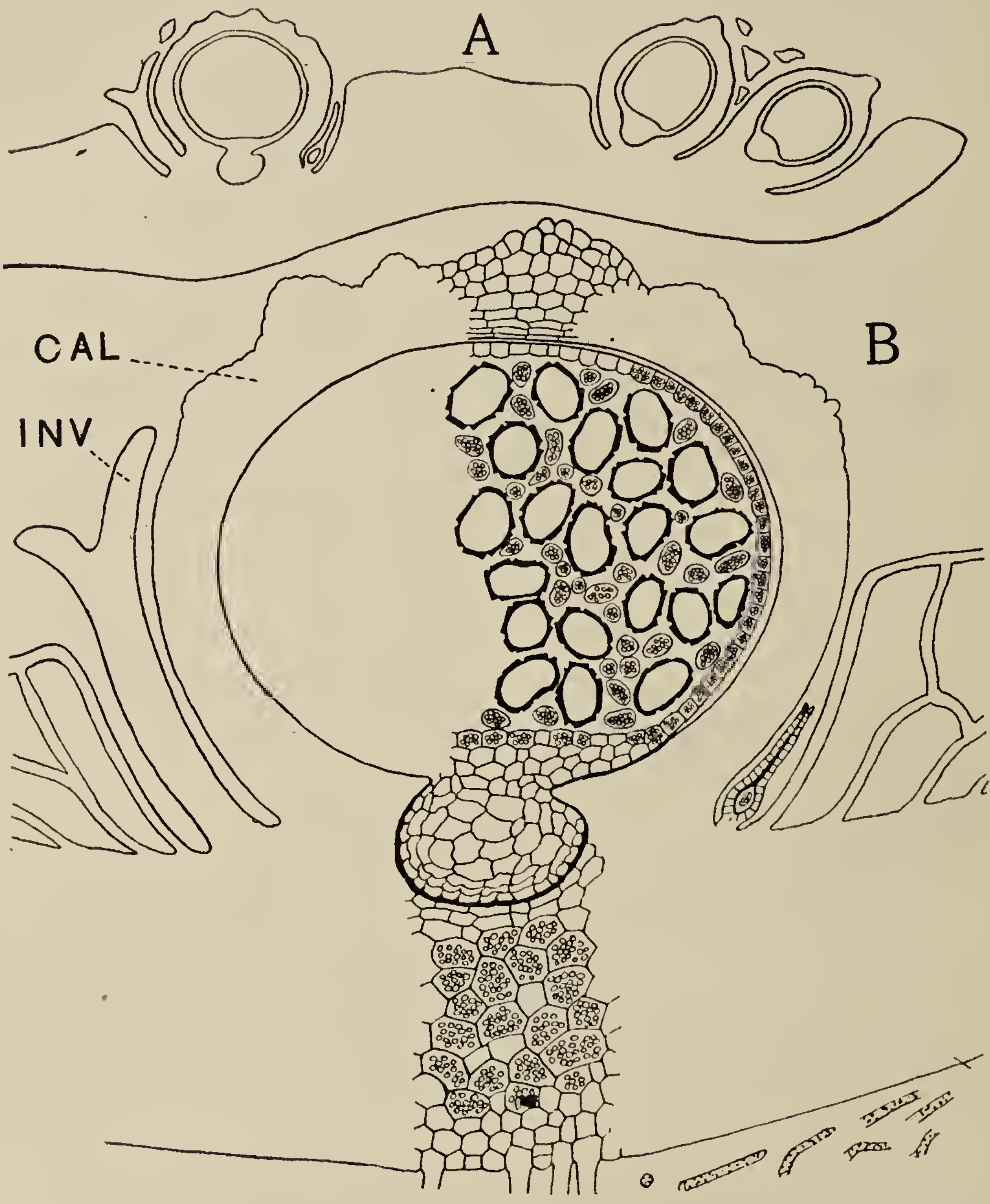


Fig. 9. *Corsinia marchantioides.* A, longitudinal section of thallus with three sporogonia. B, a part of A enlarged; *in.*, involucre; *cal.*, calyptra; mingled with the developing spores are the starch-bearing sterile cells.

Immediately behind the group there arises a hood-like outgrowth which bends forward over the archegonia (Fig. 10); this involucre is several cells thick but contains no chambers, and it is formed quite independently of fertilisation. The cells forming the capsule-wall are strengthened by U-shaped fibres deposited on the inner and radial walls; the sterile archesporial cells persist after the ripening of the spores and bear annular or spiral fibres, hence they are definite though short elaters.

Boschia lags behind *Corsinia* in the organisation of the sexual receptacles, but advances upon it in the structure of the thallus, of the capsule-wall, and of the sterile cells in the capsule.

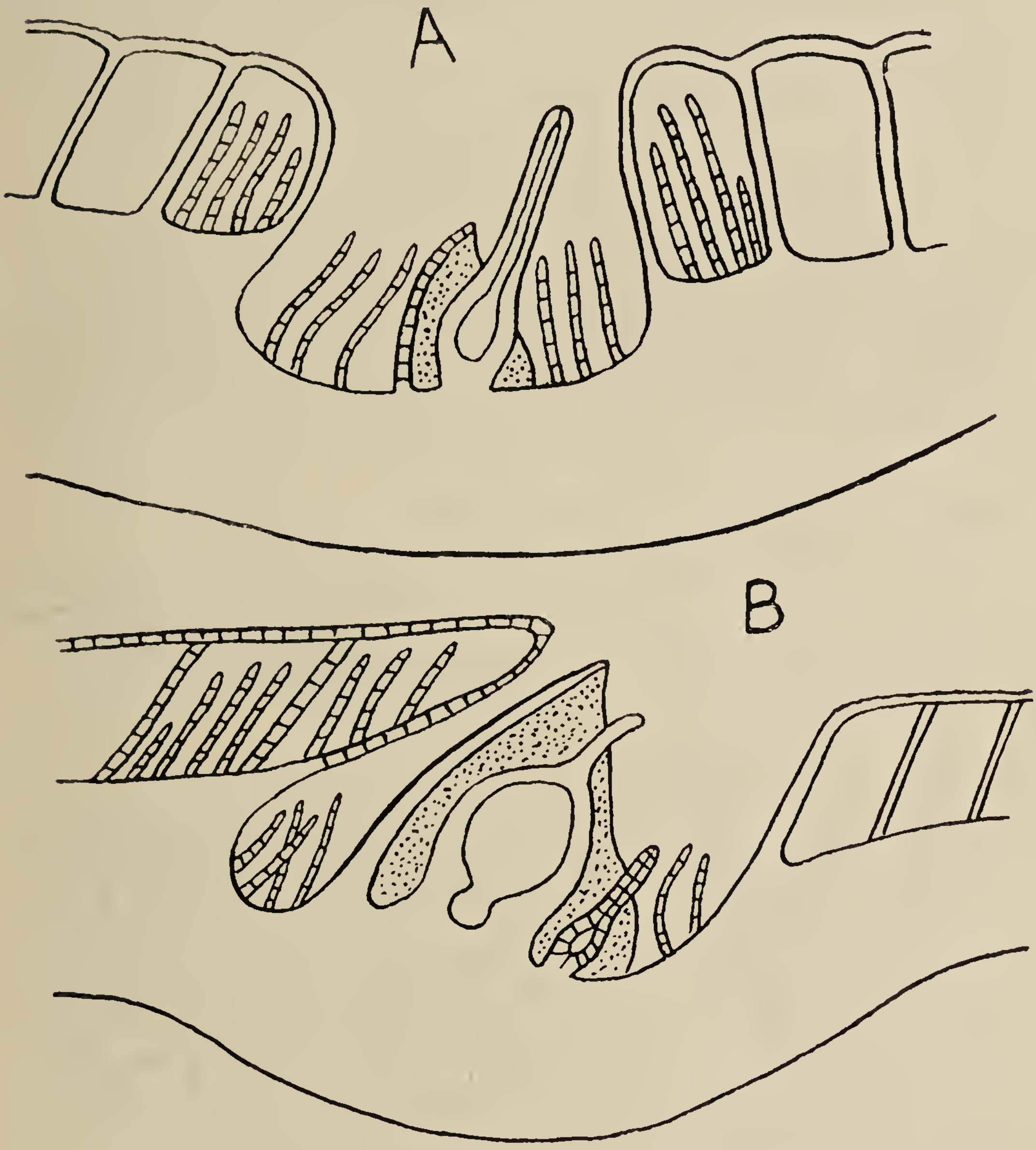


Fig. 10. *Boschia Weddelli.* Longitudinal sections of thallus. A shows the hood-like scale arising behind an archegonium; B, a later stage, with a young sporogonium. After Leitgeb.

This little group is of great interest, being transitional in various respects between the Ricciaceæ and the higher Marchantiales. One of the most interesting features is the formation of a special outgrowth for the protection of the young sporophyte. In the hood which arises behind the archegonial group in *Boschia* we have a structure which may be compared with the two-valved involucre of the Targioniaceæ and with the tubular involucre of *Monoclea*; while the umbrella-like outgrowth of *Corsinia* represents, so to speak, a belated attempt at the formation of the stalked archegoniophore, or carpocephalum, of the Marchantiaceæ (Marchantioideæ), which arises in advance of the archegonia and carries them up with it owing to basal growth and also turns them upside-down owing to growth of its expanded upper portion.

TARGIONIACEÆ.

This order contains the two genera *Targionia* and *Cyathodium*. The development of both was worked out by Leitgeb; further investigations have been made on *Targionia* by Campbell (1), Macfadden (15), Cavers (3), and Douin (7), and on *Cyathodium* by Lang (13). The chief distinguishing features of the order are the restriction of the antheridia to special short ventral branches of the thallus, and the development of an envelope, consisting of two lateral scales, around the archegonial group. The latter occupies an area immediately behind the growing-point of the thallus, the

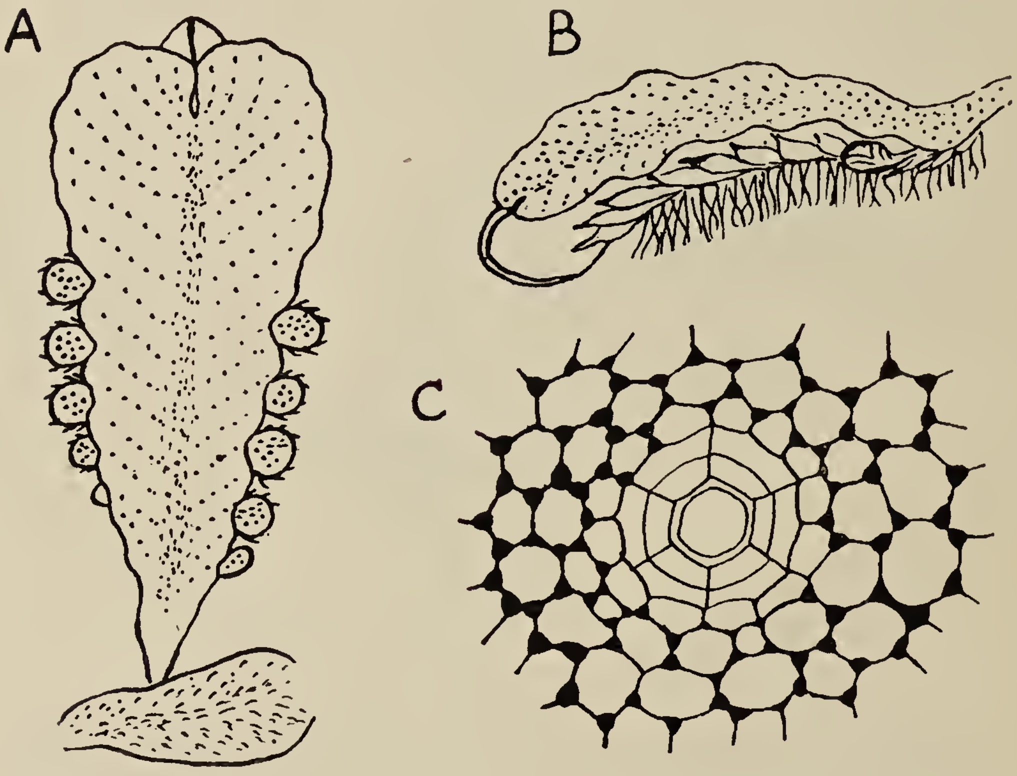


Fig. 11. *Targionia hypophylla*. A, a plant, seen from above, with male branches at the sides and an involucre at the apex; B, a similar plant in side view, showing the bivalved involucre; C, part of the epidermis, with an air-pore in surface view.

apical growth being arrested by the formation of the archegonia, so that further growth is only possible by means of adventitious branches.

In *Targionia* (Figs. 11, 12, 13) the air-chambers, arranged in a single layer, contain assimilating filaments, and the pore is surrounded by several concentric rings of cells. Each of the male branches, arising from the sides of the midrib, consists of a cylindrical basal portion and an expanded terminal receptacle. The upper surface of the latter is studded with little conical outgrowths, each traversed by a canal leading down to an antheridium-containing chamber (Fig. 12). The archegonia, formed just behind the growing-point of the thallus, are arranged in two longitudinal rows, and from either side of the group there arises a scale which grows forward and, meeting the opposite scale, forms a complete sheath over the developing sporogonium, the edges of the two scales becoming united by interlocking processes (Figs. 11, 13). The sporogonium consists of a spherical capsule, separated from the bulbous foot by a seta which eventually elongates, rupturing the calyptra and pushing apart the two halves of the involucre, exposing the upper portion of the ripe capsule in order that the spores may be dispersed. The cells forming the apical part of the capsule-wall are larger than the rest and have short elater-like cells attached to them, so that in this region the wall is two-layered, and at dehiscence

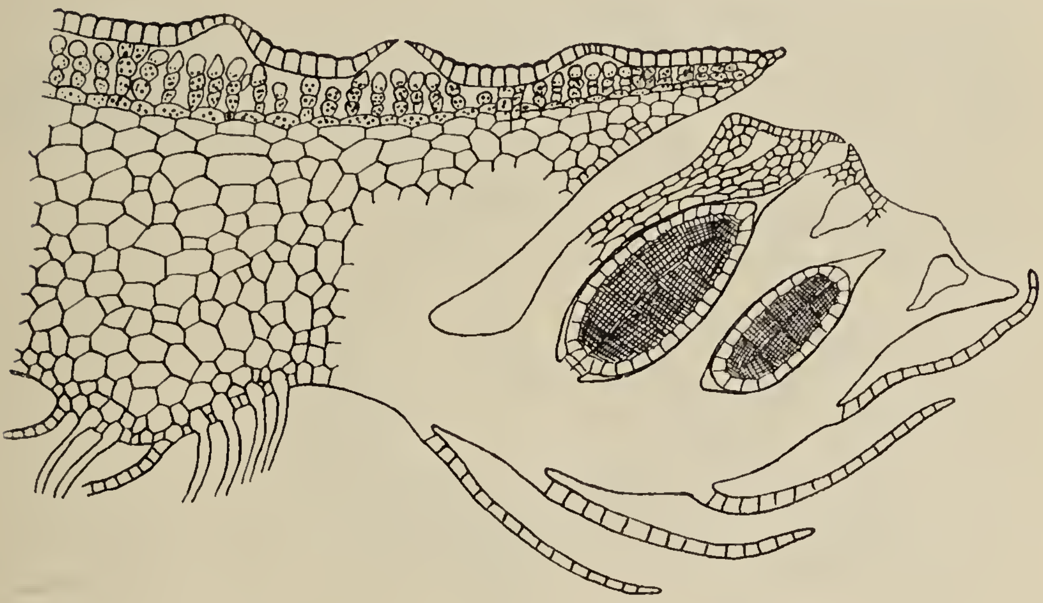


Fig. 12. *Targionia hypophylla.* Transverse section of thallus, with an antheridial branch on the right.

is detached as a lid. The elaters are well developed, mingled irregularly with the spores, and often branched. The spore mother-cells, instead of remaining spherical or ovoid as in the other Marchantiales (except *Monoclea*), become deeply divided into four lobes (as in Jungermanniales).

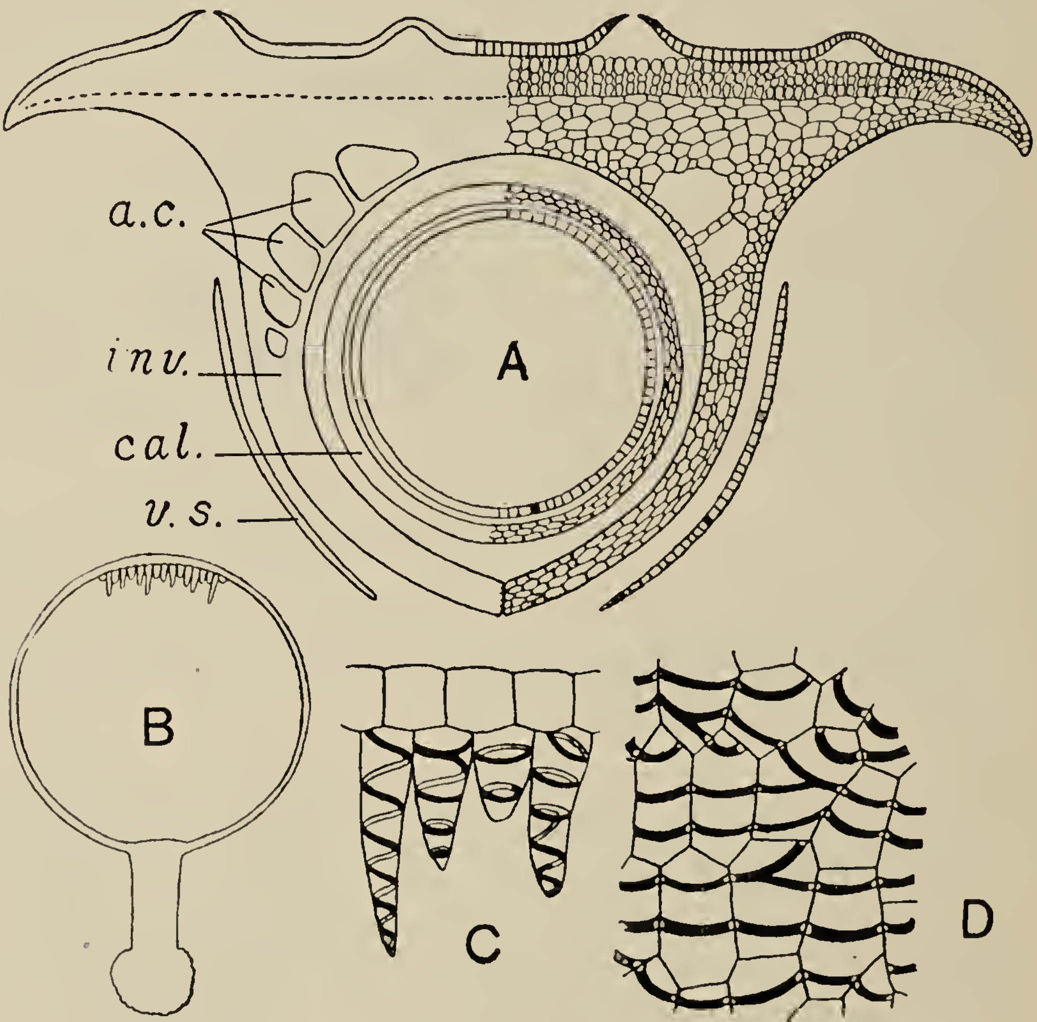


Fig. 13.—*Targionia hypophylla.*

Fig. 13. A.—Transverse section across the anterior end of a fruiting plant, showing a nearly mature sporogonium enclosed in its calyptra (cal.) and surrounded by the two-lobed involucre (inv.), the tissue of which contains air-chambers at the base (a.c.). Outside of the involucre, two ventral scales (v.s.) are shown. The upper part of the section shows the ordinary structure of the thallus. ×35. B.—Median longitudinal section of a nearly mature sporogonium, showing the spherical capsule, short seta, and bulbous foot. The spores and elaters are omitted, to show more clearly the apical patch of fixed elater-like cells. ×35. C.—Part of B., showing some of the elater-like cells at the apex of the capsule. ×300. D.—Part of the ripe capsule-wall, showing the annular fibrous bands on the walls of the cells (surface view). ×300.

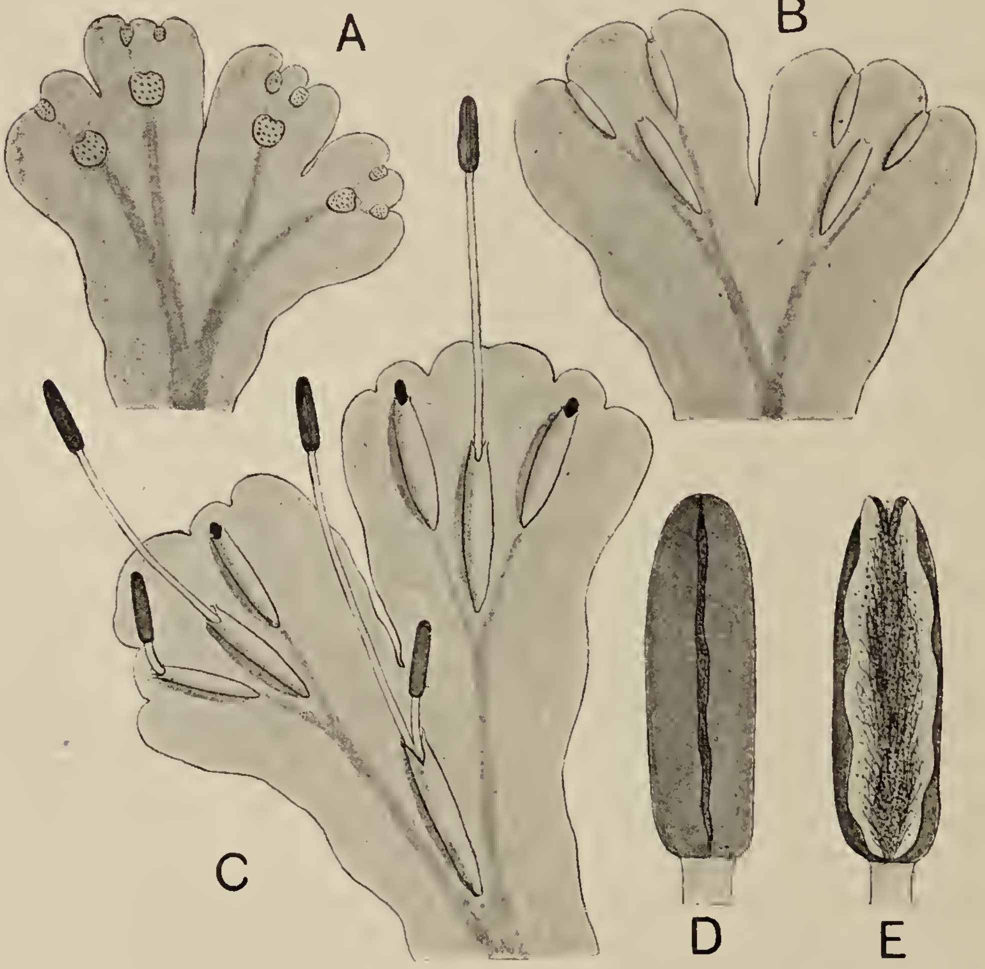
Cyathodium is closely allied to *Targionia*, and the structural differences in the thallus which separate the two genera are chiefly attributable to their very different habitats. *Targionia* is xerophilous, with well-developed thallus, assimilating filaments, and thick epidermis; *Cyathodium* grows in moist and shaded places and shows markedly hygrophilous characters. Lang investigated *C. foetidissimum* (the largest and least reduced species, with well-defined air-chambers and with tuberculate as well as smooth-walled rhizoids) and *C. cavernarum* (the most reduced species, with less regular air-chambers, no distinct midrib, inconspicuous ventral scales, and no thickened rhizoids). The thallus consists for the greater part of a single basal layer of cells, upon which are borne the air-chambers. The latter contain no filaments, and the thin-walled epidermal cells have strongly convex upper and lower walls, probably serving as lenses to collect the feeble light in which the plant lives. The male branches and the archegonial receptacles have much the same structure as in *Targionia*. The capsule has a well-developed apical cap, and the seta consists of only two or four rows of cells. For details, reference should be made to Lang's extremely interesting paper (13).

MONOCLEACEÆ.

The genus *Monoclea*, of which two species are distinguished by systematists (*M. Forsteri* in New Zealand, *M. Gottschei* in tropical and South America), is one of the most interesting among the Hepaticæ. The genus was founded by Hooker (11) for a plant discovered by Forster during Captain Cook's famous voyage and named by Forster "Anthoceros univalvis." Hooker showed that the plant was no *Anthoceros*, since its oblong capsule has no columella and opens by a single slit, giving it a spoon-like appearance. Gottsche (9) described the minute structure of the thallus, noting the presence of two kinds of rhizoids (some wide and thin-walled, others narrow and thick-walled) and the occurrence of fungal hyphæ in the lower tissue, the structure of the ripe sporogonium, the one-layered capsule-wall, and the long spirally thickened elaters. Later, Gottsche (10) discovered the oval cushion-like male receptacle in plants from Mexico. Leitgeb[1] noted that the thick-walled rhizoids are distributed over the whole underside of the thallus and lie parallel with it, while the thin-walled ones arise only from the thicker middle portion of the thallus and stand out at right angles to it. He concluded that *Monoclea* is more closely related to *Pellia* than to any of the Marchantiaceæ, though it

[1] Unters., III., p. 62; VI., p. 130.

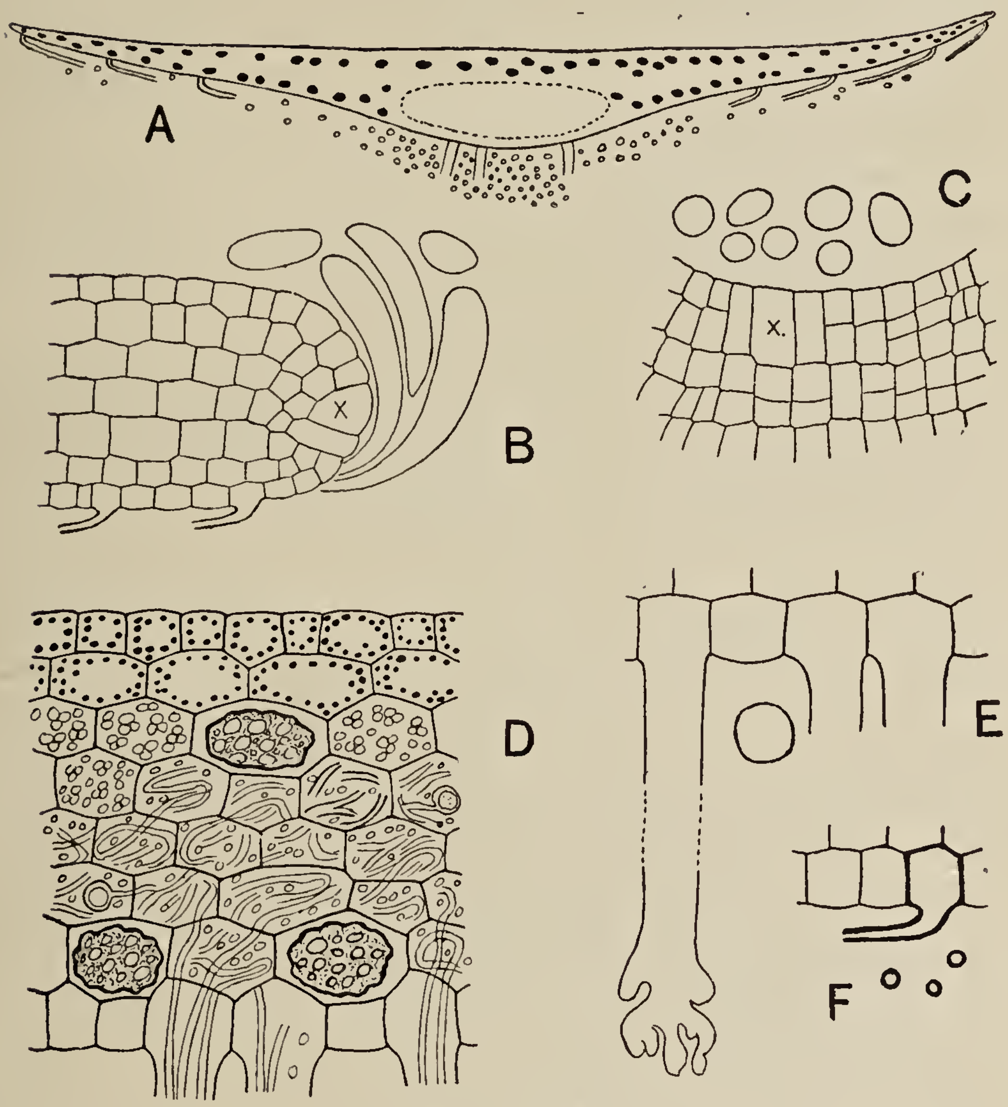
resembles the latter in the possession of a cushion-like male receptacle, which he likened to that of *Fegatella*. Schiffner, who had evidently overlooked the later papers of both Gottsche and Leitgeb (since he says the male plant is unknown), places the genus in the Anacrogynous Jungermanniales, beside *Pallavicinia* and *Symphyogyna*. Ruge (17) found that in the development of the antheridium several transverse walls appear before any longitudinal ones appear. Campbell (2), reviewing the work of the writers above-mentioned, concluded, from the presence of two types of rhizoids, the development of the male receptacle and the antheridium, and his own observation that the archegonium neck has six rows of cells, that *Monoclea* should be transferred to the Marchantiales and placed near *Targionia*. The writer (3, 4), from his examination of



Monoclea Forsteri.

Fig. 14. A., Male plant, × 1. B., Female plant, × 1. C., Female plant, in which three capsules are exserted, × 1. D., Ripe capsule, showing dehiscence by a single longitudinal slit, × 4. E., The same, later; the margins have rolled back, exposing the mass of spores and elaters; × 4.

abundant fresh New Zealand material, was able to add various



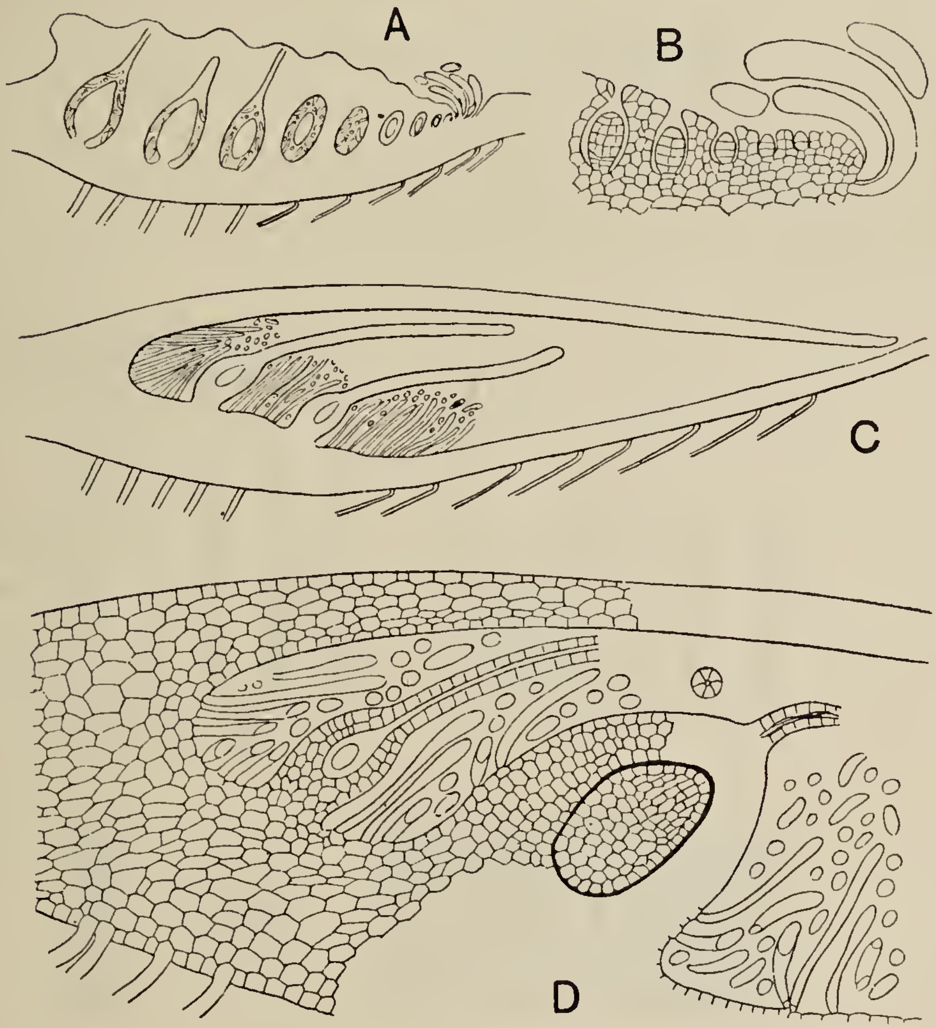
Monoclea Forsteri.

Fig. 15. A.—Transverse section of thallus. The large dots indicate the oil-bodies, the dotted line the position of the mycorhiza. The narrow rhizoids are shown mostly in cross section, the wide ones (of which three are shown) are only borne on the median portion of the thallus. ×15. B.—Vertical longitudinal section through the growing-point of the thallus, showing the apical cell (x) and the large club shaped mucilage-hairs; on the lower surface behind the apical cell are shown two of the narrow rhizoids. ×120. C.—Horizontal section through the growing-point, showing the apical cell (x) and its segments, with the large mucilage-hairs in cross-section. ×120. D.—Part of A., traversing the mycorhizal zone, the cells of which contain branching fungal hyphæ, some of the latter being shown in the rhizoids. Three of the oil-containing cells are shown; the cells above the mycorhiza contain starch-grains, and the two upper layers of cells contain chloroplasts. ×120. E.—Part of a vertical section of the thallus, showing three of the wide thin-walled rhizoids; on the left the branched free end of a rhizoid is shown.. ×120. F.—Part of a section showing one of the narrow thick-walled rhizoids in longitudinal section, and three others in cross section. ×120.

details, including the occurrence of large oil-bodies filling certain cells of the thallus, the presence of a row of initial cells at the growing-point, and the formation of an octant-stage in the embryogeny—all of which are characteristic of the Marchantiales as distinguished from the Jungermanniales; the male receptacle was shown to differ from that of *Fegatella* (which it superficially resembles) by having a single anterior growing-point, as in the lower Marchantiales. A little later appeared a detailed paper by Johnson (12) on material collected in Jamaica, in which it was shown that the narrow rhizoids have the tubercles characteristic of the corresponding rhizoids of Marchantiales.

The thallus (Fig. 14) has a perfectly smooth upper surface, and there are no traces of air-chambers; while the only appendages on the lower side, in addition to the rhizoids, are the long club-shaped hairs which bend up over the growing-point (Fig. 15). The absence of chambers and of ventral scales, and the feeble development of tubercles in the narrow rhizoids, may be correlated with the extremely hygrophilous habitat of the plant. Coker (6) has shown that plants of *Dumortiera hirsuta* (allied to *Marchantia*) growing on porous sandy soil had well-developed air-chambers, while other plants that were constantly wet with dripping water had no trace of chambers. In *Dumortiera irrigua*, chambers are formed at the apex of the thallus, but soon become disorganised and are represented in the older parts only by the remains of the vertical walls, which form a network. Campbell (1) found that in *D. trichocephala* no trace of chambers can be detected even at the apex of the thallus. Hence in this hygrophilous genus we find every stage in the reduction of the chambers, related to the conditions of the habitat. Even in *Marchantia* itself, submerged plants or branches show a similar reduction of the chambers; and in *Fegatella* the writer (5) found that the submerged form had greatly reduced ventral scales and hardly a trace of tubercles in the rhizoids borne in the axils of the scales.

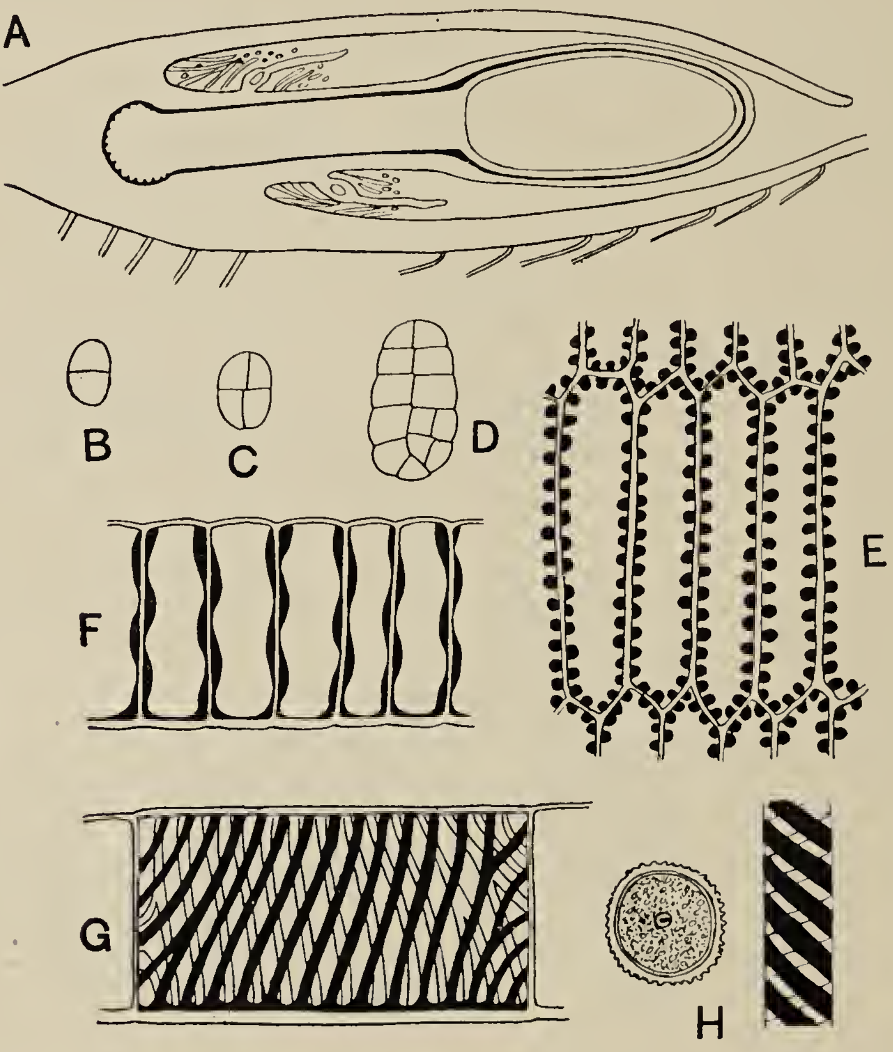
The only objections that can be urged against placing *Monoclea* in the Marchantiales are found in the position of the archegonia and in the form of the mature sporogonium. The archegonia are developed in a pit (Fig. 16) which becomes drawn out to form a long tube, much as in *Pellia*. However, the development of the tubular involucre of *Monoclea* is not in reality widely different from that of the hood-like involucre of the Corsiniaceæ or the two-lobed involucre of the Targioniaceæ. In these plants, as in *Monolcea*, the archegonia are produced on an unspecialised portion of the thallus, and the form of the involucre depends merely upon the amount of the surrounding tissue which grows out and the rate at which it grows forward over or around the group of archegonia. Thus there is no real difficulty in homologising the involucre of *Monoclea* with that of the Corsiniaceæ and Targioniaceæ. The three families stand apart from the Ricciaceæ on one hand and the Marchantiaceæ on the other with regard to the arrangements for the protection of



Monoclea Forsteri.

Fig. 16. A.—Part of a vertical longitudinal section of a male plant, traversing a receptacle. The walls of the antheridial cavities bear numerous club-shaped mucilage-hairs, and much larger hairs are borne at the anterior end of the of the receptacle, on the right. On the left are shown five of the wide rhizoids which grow downwards ; on the right, six of the narrow rhizoids which grow back parallel with the lower surface of the thallus. ×20. B.—Part of a similar section, showing the growing-point of the receptacle, with the large mucilage-hairs and several developing antheridia. ×90. C.—Part of a vertical longitudinal section of a female plant, traversing a receptacle. Between the archegonia arise numerous long mucilage-hairs ; rhizoids as in A. ×35. D.—Part of a similar section, showing a fertilised archegonium containing an embryo, and on the left of this an unfertilised archegonium. ×90.

the archegonia and the developing sporogonia. In Ricciaceæ each archegonium is simply sunk in a cavity of the thallus; in the Marchantiaceæ they are carried up on stalked archegoniophores, besides being protected, singly or in groups, by involucres; while in the three intermediate families they are developed in groups on the free surface of the thallus and are protected by the hood-like outgrowth of the surrounding tissue.



Monoclea Forsteri.

Fig. 17. A.—Longitudinal section through a receptacle containing a half-ripe sporogonium, covered by the calyptra, on the sides of which, towards the base, are borne the unfertilised archegonia and some of the mucilage-hairs. ×35. B., C., D.—Young sporogonia in longitudinal section. ×90. E.—Part of the capsule-wall in surface view (outer surface), showing the ends of the fibrous thickenings on the vertical walls of the cells. ×200. F.—Part of the capsule-wall in transverse section. ×200. G.—A cell of the capsule-wall, from a longitudinal section of the capsule, showing the two sets of fibres crossing each other on the cell-wall. ×200. H.—Spore in section and part of an elater in surface view. ×700.

It must be admitted that the habit of the sporogonium, with its long seta and its erect cylindrical capsule, differs greatly from that of any of the other Marchantiales. Apart from the embryology, which is of the Marchantia-type, *Monoclea* agrees with all known Marchantiales and differs from all Jungermanniales (except the Calobryaceæ) in that the capsule-wall is a single layer of cells in thickness (Fig. 17). Moreover, the great length of the seta may perhaps be related to the extremely hygrophilous habitat, enabling the capsule to be raised well above the wet substratum for the dispersal of the spores. In the Marchantiaceæ, where the sporogonia are raised well above the thallus by the stalked archegoniophore, there is no necessity for a long seta, and accordingly the latter simply elongates sufficiently to thrust the ripe capsule through the calyptra. It would appear reasonable to suppose that *Monoclea* represents a blindly-ending line of development arising from forms like the Corsiniaceæ or the Targioniaceæ—a line in which the sporogonium itself has assumed the function of thrusting the capsule upwards. In the main line of the Marchantiales, which leads from these lower forms to the Marchantiaceæ, this function has devolved upon the outgrowth (archegoniophore) of the thallus which carries up the group of fertilised archegonia.

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(To be continued).

THE WOODLANDS OF ENGLAND,

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Introduction.

The present paper is an attempt to deal, in a general way, with the character and distribution of the different types of natural and semi-natural woodland in England. It is a direct outcome of the work of the Central Committee for the Survey and Study of British Vegetation, formed at the end of 1904,[1] with the object of bringing into intimate association the various workers engaged in active study in the field of the nature and distribution of British vegetation.

Before passing on to our special subject it will be useful to deal quite shortly with the method of vegetation study and representation adopted by the Committee in what they term "primary" survey of vegetation, and also with certain objections to this method of treating vegetation, which may perhaps be entertained in some quarters.

The method of primary survey employed by the Committee was originally adapted by the late Robert Smith, of Dundee,[2] from the system of cartography worked out by that acute plant-geographer, Professor Flahault of Montpellier,[3] whose pupil Smith was. A limited area of the country, either a natural physiographic region, or an area corresponding with one or more sheets of the "one-inch" Ordnance Survey map (1 : 63,360), having been selected for survey, the different types of natural and semi-natural vegetation, and also the "artificial" types, such as farmland, plantations, and parks, occurring within the area, are distinguished

[1] New Phytologist, IV., 1905, p. 23.

[2] Botanical Survey of Scotland: I., Edinburgh district. Scottish Geogr. Mag., 1900.

[3] Ch. Flahault, Essai d'une carte botanique et forestière, etc., Ann. de Géogr., 1891.

and recorded on a map by means of different colours, so far as the scale of the map will allow. In the memoir accompanying the finished vegetation-map, the characteristics of each type are analysed, lists of constituent species are given (in which "dominant" are distinguished from "subordinate" species), the transitions between, and mutual relations of, the different types, and the connexion of each with soil and climatic characters and with the geological structure of the country are discussed; while the displacement of one type by another, and so far as possible the relations of each to forestry and agriculture, the two great industries directly based upon the conditions determining natural vegetation, are dealt with. The successive memoirs published by members of the Committee show progress in all these directions. This progress is due to the gradual extension of the survey to fresh regions, to the comparatively large areas which can be dealt with by the method, to increased insight into the real nature and relationships of the different types, and finally to the close co-operation rendered possible by the existence and frequent meetings of the Committee, both round the table and in the field.

The study on these lines of the British woodlands, though by no means complete, has now reached a stage at which a general presentation of the subject has become possible; and the present paper will, it is hoped, serve a useful purpose by making available to a wider circle some of the more general results in one branch of the Committee's work. As time goes on, it is proposed to deal in a similar way with other types of vegetation, such as grassland, heath, moorland, freshwater marshes, salt marshes, and sand dunes.

THE STATUS OF BRITISH WOODLANDS.

It is desirable at the outset to present our conclusions as to the *status* of British woodlands in general.

In a country like England, much of which has been cultivated and comparatively thickly populated for centuries, it may be asked, do there remain any natural woodlands at all? Have not existing woods been so altered by planting and in other ways that they no longer represent the native plant-communities, but are rather to be considered as mere congeries of indigenous and introduced species?

It is undoubtedly true that there is little "Urwald" or true virgin forest remaining in the country, though some of the woods, especially near the upper limit of woodland in the more mountainous regions, might make good their claim to this title. On the other hand, there are, of course, many plantations pure and simple which have been made on moorland, heath, grassland, or arable land, and which may of course consist of native or of exotic trees or of a mixture of the two. But between these two extremes, according to the conclusions of all the members of the British Vegetation Committee who have given any special attention to this subject, come the great majority of the British woods; which are neither virgin forest, nor plantations *de novo*, but are the lineal descendants, so to speak, of primitive woods. Such semi-natural woods, though often more or less planted, retain the essential features of natural woods as opposed to plantations, and without any reasonable doubt are characterised by many of the species which inhabited them in their original or virgin condition.[1]

We may, in fact, construct a series leading from the one extreme of virgin forest to the other extreme of artificial plantation on open ground. Thus we may distinguish the following types:—

(1). Primitive woodland which rejuvenates itself naturally, from self-sown seed or vegetatively, and in which felling has been, at the most, quite occasional and sporadic, and confined to isolated trees. Here we may place with confidence some of the woods of *Quercus sessiliflora* and of ash, which occur on the Pennines and in the Lake District.

(2). Native woods in which there has been little or no planting, but in which fairly regular felling takes place, the woods rejuvenating themselves naturally from self-sown seed, or in the case of the oak, partly from the stools. Here we may place some of the beechwoods of the Chilterns, certain small remnants of the old oak-forest of the Weald, dominated by *Q. Robur* (=*Q. pedunculata*), and some of the ashwoods of Somerset and north-east Yorkshire. The ground vegetation of such woods is no doubt primitive; though after extensive felling, light-demanding plants often invade the clearings, just as they constantly colonise the open "rides" or "drives" of a wood; and just as, even in a tract of virgin forest, species invade the more open portions from neighbouring plant-associations. These species, however, tend to disappear as the wood grows up after the "fall."

(3). Woods which are regularly planted up, after felling, with the species of tree originally dominant. This is often done when the ground is completely cleared of trees and shrubs, because, under such conditions, natural rejuvenation is sometimes a slow and uncertain process, particularly in the case of the hardwoods. This kind of wood differs but little ecologically from the second type.

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[1] The system usually followed on estates has been first to "improve" (but not replace) the existing woods. Even the parklands round the great houses have had their characters determined by the woodland natural to the soil.

(4). Woods planted up, after felling, with a mixture of species, consisting partly of the natural trees, partly of other species, indigenous or exotic. Unless the planted species markedly differ in light-demand from the natural ones, the artificial element does not materially alter the character of the ground vegetation. If they do so differ, the composition of the ground flora is necessarily changed to a certain extent.

(5). Woods entirely planted, after felling, with species distinct from the original ones, *e.g.*, Larch replacing Oak. Here again the change in the flora depends on the character of the planted trees, and on the distance apart at which they are planted. The change may be very slight or very pronounced, but the relation of the ground flora to that of the natural woods on the same type of soil is generally quite evident.

(6). Plantations on arable land, grassland, or heath. These, when recent, are quite easy to distinguish from natural or semi-natural woodlands, because the ground flora, after the plantation has grown up, is floristically poor, and does not consist of typical woodland species. How far such woodland species may colonise plantations which have been made on open ground, and how long it takes to complete colonisation so that a plantation becomes indistinguishable from a natural wood, are questions on which practically no data, so far as we know, are at present available.

Of these types, the second and third are to all intents and purposes natural woods, and they are always treated as such in our surveys. With regard to the fourth and fifth types, there may, in some cases, be a certain amount of doubt and difficulty in assigning by inspection a given wood to one of these types ; but the difficulty is much less in practice than might be supposed, and for a reason that will appear immediately.

Woods that are completely replanted with species of trees different from the natural woodland trees characterising the given soil, climate, and geographical position, are distinguishable simply because they are composed of trees different from those forming the bulk of the woods of the district, so far as they are on the same type of soil. When, however, the same association of trees occurs, forming wood after wood on the same type of soil, it may be concluded with reasonable certainty that we have the natural type of woodland for the given type of soil in the given climate and geographical position. It is impossible to suppose that by chance or design the whole of the woods on a given rock over a very considerable extent of country have been replanted with the same species, other than the natural ones; especially when it is observed that on a neighbouring rock, producing a different kind of soil, quite a different type of wood is found, while in another part of the country, on a rock belonging to a different geological formation, but lithologically similar and producing the same kind of soil as the first one, the same type of wood occurs as in the first case. It is this actually observed constancy in the general type of woodland on a given type of soil over wide, and often widely separated, stretches of country, which leads to the conclusion that the greater part of the existing woodlands of England largely retain their original character.

It might perhaps be urged that if some tree, other than the natural one, were found to be particularly suitable for a given kind of soil, this tree would, in course of time, come to be planted in all the woods on that soil. To such an argument we would make two rejoinders. First, there is no evidence whatever that such planting —so widespread and systematic as to lead on this theory to the observed results—has ever been carried out in this country. Secondly, as is well known to foresters, the majority of our native trees will flourish quite well, planted on a great variety of soils; so that the supposed gradual selection of the economically best tree for a given soil, would not in fact work out so as to produce the actual distribution. The success of a tree-crop when planted on a given soil is of course quite a different thing from the *natural dominance* of a tree on the same soil. A species which may succeed perfectly well when planted on a certain soil, would have no chance of survival when placed in competition with the natural dominant. Hence the economically best native species is by no means necessarily the same thing as the natural dominant. Evidence of natural dominance is therefore of importance in this connexion; and when such evidence is forthcoming and is associated with the uniformity above mentioned, we may conclude with perfect safety that the actually dominant tree is the natural primitive wood-forming tree on the soil in question, even if (as is very often the case) it is now regularly re-planted.

Exceptional cases, it is true, occur. Thus the Scots pine is now the natural dominant on many of the sandy soils of southern England, as on the Eocene sands and overlying "plateau gravels" in both the London and Hampshire basins, and on much of the Lower Greensand fringing the north and west of the Weald. There is good evidence, however, of the widespread introduction of the Scots pine into southern England in the eighteenth century, if not earlier. This tree is undoubtedly particularly well suited to the soils in question, and it has spread and is still spreading over the heaths of these regions by means of self-sown seed. On the Lower Greensand, however, the pinewoods alternate with oakwoods; on the shallow soils with woods of *Quercus sessiliflora* mixed with birch and beech, all three undoubtedly native trees in the south of England; and we cannot therefore hastily conclude that Scots pine is the original dominant on these soils.

These considerations lead us to believe that woods belonging to the fifth type, *i.e.*, those in which the original species have been entirely replaced by others, are in most cases not really difficult to identify. The species actually present differ from the regular type for the given soil and climate. The same criterion will also apply to woods belonging to the fourth type. The scattered "aliens" are identified because they are not the regular associates of the dominant on the soil in question, or because of their known history, or because of their general geographical distribution. There are of course some difficult cases here also; but they are certainly far fewer than might be expected by those who have no experience of the kind of knowledge obtained by the systematic exploration of the plant associations of a given region, and their comparison with those of other regions.

One general conclusion at which we have arrived is that the existing English woodlands have for the most part been altered in their essential characters to an extent which may appear surprisingly slight to those unfamiliar with the actual facts of distribution. This is no doubt largely due to the innate conservatism of the English landowner, as well as to the backward state of forestry practice in this country.

COPPICE AND "COPSE."

A general feature of the woodlands of southern England, as opposed to those of the north, is the great prevalence of coppiced or partially coppiced woods.[1] The coppice, mostly of hazel, though also of oak, ash, and birch, sometimes of beech, locally of hornbeam, in marshy woods frequently of alder and willow, and, particularly in the hop-growing districts of Kent, often of Spanish chestnut, is typically cut once in ten to twelve years, or less generally at longer intervals.[2] In most of the coppices there are standard trees, usually oaks, not grown in close canopy, but more or less isolated, so that each standard acquires the branching habit characteristic of a tree grown in the open. This method of cultivation, which is some centuries old, gives rise to a distinct and *quasi*-artificial type of woodland, known to foresters as "copse" or "coppice with standards."[3]

The prevalent type of copse is the oak-hazel copse, and, as will be seen in the sequel, this is derived from more than one of the natural types of woodland. It is by far the commonest form of woodland over wide areas in southern England, owing to the great demand in past times for hazel for hurdles and fencing, cask-hoops, etc., and for oak timber for the navy and various other purposes, as well as for oak-bark used in tanning. These demands have greatly diminished and in some cases practically disappeared during the latter half of the nineteenth century, and at present this type of wood is but little if at all remunerative. Their continued existence is due partly to the conservatism already referred to, and partly to the fact that they are very convenient for pheasant-covers, for which purpose they are almost invariably used.

The ground vegetation of the oak-hazel copse shows a regular periodicity of development, dependent upon the regular cutting of the coppice. Towards the close of each cycle, when the coppice has grown up, the dense shade cast by the bushes reduces the ground vegetation to a poor state. Extreme shade-plants alone can flourish under such conditions, and the ground is but sparsely dotted with leafy plants, many of which are unable to flower. After the coppice is cut, the access of bright light provides a great stimulus to development; and the previously dormant or weakly vegetating plants spring into activity. About the second or third season after cutting, the ground vegetation attains its maximum development; and, as is well known, the floor of the wood is often covered in April and May with sheets of such showy species as primroses, bluebells, wood anemones, or red campions. As the new coppice shoots grow up from the stools, this active vegetation lessens in vigour, and gradually returns to its former condition.

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[1] In certain districts of the north coppicing on a large scale is met with, as in the Furness district of Lancashire, and also in central Scotland. This is generally in relation to a definite economic demand.

[2] In parts of Cornwall, the extensive oak-coppices are cut once in about twenty-five years, and, towards the end of the rotation period, have the appearance of dwarf high-wood in close canopy.

[3] See Nisbet, "Our Forests and Woodlands," London, 1900, where the distinction is made between *copse*, *i.e.*, "coppice with standards," and *coppice*, without standards. This distinction is so convenient that we have adopted it in the present paper, but it does not seem to be in general use among foresters.

RELATIONS OF CLIMATE AND SOIL.

If we assume the position adopted in this paper, that the great majority of the existing British woodlands may be regarded as natural or semi-natural plant associations, *i.e.*, as being the descendants, more or less modified, of the various primitive types of forest that existed in this country, and as bearing unmistakable marks of their origin, we have to enquire what are the factors which determine the distribution of the different types. An intimate scientific knowledge of these factors no one can pretend to possess, but a certain amount of information may be gained by considering the observed distribution in relation to the different characters of the environment.

If we consider first that class of environmental conditions usually comprised under the general term *climate*, we find that we may distinguish two kinds of climatic variation.

First we have the variation met with in passing across the country at a relatively slight elevation above sea level, as exemplified by the difference between the climate of Kent, for instance, and that of the Lake District, or between the climate of Cornwall and that of East Anglia. These differences in climate, considerable as they are, have for the most part an effect on the secondary characters only of the English woodland associations, *i.e.*, on the presence or absence of certain associated species. They do not alter, except in the manner to be indicated presently, the general nature of the woodland types. For example, the type of woodland which occurs on the Jurassic marls of Somerset is identical with that which occurs on the chalky Boulder-clay of East Anglia, but in the Somerset woods ferns are much more numerous both in species and in individuals than in East Anglia, and this difference is certainly due to the difference of climate. Of other differences in the associated species we cannot yet say whether they are due to climate or not, and we therefore class them as "floristic" differences. For instance, we may cite the occurrence of such western species as *Lithospermum purpureo-coeruleum* in the Somerset and not in the East Anglian woods, and of such eastern species as *Primula elatior* in the East Anglian and not in the western woods of this type.

In the second place we have the difference of climate met with in ascending a hill-mass of considerable altitude. In the north of England, we find a noticeable effect on the vegetation at a height of about 1,000 feet (see p. 135). None of the south-eastern hills is high enough to produce any appreciable difference of vegetation from this cause.

When we turn to the second group of environmental factors, those concerned with soil, we meet, on the other hand, with the principal factors which actually differentiate the British woodland types.

Briefly, we find that the Alder-Willow series is characterised by a very high water-content, and that the other two principal series which we distinguish, the Oak and Birch series on the one hand and the Beech and Ash series on the other, are related to the lime-content of the soil. When, however, either of these two series is subdivided, we find that the subdivisions are related to the water-content and to the humus-content of the soil. Further, the nature of the humus formed in the various soils has an important influence on the character of the sub-types in the Oak and Birch series; and finally the available food (in the shape of mineral food-salts) may perhaps be decisive in determining the success or failure of certain tree-associations on sandy soils.

Though the way in which the chemical factors, or the correlated physical factors, affect the vegetation—long a subject of controversy among plant-geographers—lies outside the scope of the present paper, there is an interaction of soil and climate to which we must call attention. The amount of water held by the soil in a given climate (*i.e.*, with a given rainfall and rate of evaporation) depends primarily upon the texture of the soil; but with a wetter climate, *i.e.*, with increased atmospheric moisture and with greater precipitation, especially a rainfall distributed over a greater number of days in the year, the average amount of water actually present in a soil of given texture is greater. Thus a "light" or relatively coarse-grained soil, that would bear a "dry" type of woodland association in a relatively dry climate, may bear a "damp" type of woodland in a very moist climate.

THE CLASSIFICATION OF ENGLISH WOODLANDS.

We may now turn to a consideration of the main types of natural and semi-natural woodland that can be distinguished in this country.

Three main series may be recognized, namely, (I) the ALDER-WILLOW SERIES, (II) the OAK AND BIRCH SERIES, and (III) the BEECH AND ASH SERIES. The woods which belong to the first series are characterised by a very wet soil: those which belong to the second series are characteristic of siliceous soils whose proportion of lime is low; and those which belong to the third series are characteristic of soils which contain a considerable proportion of lime. In the bottoms of river valleys, the woods of the first series often pass gradually into those of the second and third series; and at comparatively high altitudes (300 metres), the woods of the second and third series exhibit a tendency to assume similar features; but, in general, the three series are well-defined, easily distinguished, and sharply marked off from each other.

I.—ALDER-WILLOW SERIES.

From the nature of the situations in which they are found, woods of this series do not now cover wide tracts of country, though it is probable that before the extensive drainage and cultivation of alluvial regions they were both numerous and extensive. The examples of these woods which still continue here and there, always at low levels, as along the banks of the slow streams of the New Forest, in the remoter valleys and lowland peat moors of the north of England, and in the fens of Norfolk, furnish some idea of the constitution of the primitive wet woodlands of the country.

The material for a proper understanding of the composition of this series is fragmentary; but what there is to hand points to the conclusion that the series includes at least two distinct plant associations. Thus the "carrs" of Norfolk, which are fed by alkaline and calcareous waters, harbour several woody species, such as *Rhamnus catharticus* and *Viburnum Lantana*, which are characteristic of chalky and limestone soils; while such "calcicole" species are absent from the alder-willow thickets which occur on soils fed with neutral or acidic waters. In the eastern portions of the New Forest, especially between Lyndhurst and Beaulieu, close thickets of the latter type are striking features of the landscape, as they follow, sometimes discontinuously, the courses of the streams across the sterile soils of the Calluna-heath. In some places, they form a narrow fringe on the river alluvium; while in other cases, they appear as extended islands enclosed within the valley peat moors which have arisen subsequently to the woods as a consequence of stagnation of the ground water. Within these gloomy thickets, heavy with moisture, grows a rank vegetation allied to that of marshes and almost hiding the numerous rotting trunks of fallen trees. In the course of time, as a result probably of decreasing aeration of the soil, the marshy vegetation gains the upper hand: the former woodland becomes submerged, and leaves only a sub-fossil tree-layer in the peat of the newly formed moor.

In the Furness district of north Lancashire and in the adjacent parts of Westmorland, alder-willow thickets of a similar character appear on the margins of the lowland peat moors, where the "moss" abuts on the "hard land." Here, above estuarine silt deposited in the long, narrow, tidal inlets, extensive peat moors have grown. On their edges, the drainage from the upland has been impeded; and the natural woods consequently belong to this series. As the level of the peat rises, the soil of the alder thickets encroaches on the adjoining oakwoods, whose ground vegetation gradually gives place to the advancing wet moorland associations.

Of a different nature, and arising subsequently to the deposition of the peat, are the "carrs" of the Norfolk fens. These may be subdivided into *fringing carrs* which line the banks of some of the "broads," and *fen-carrs* which occur on older peat. Alder and *Salix cinerea* are abundant in both types. Species of Ribes are abundant in the former; while *Salix repens*, *Myrica Gale*, *Rhamnus Frangula*, *R. catharticus*, *Viburnum Opulus*, and *Ligustrum vulgare* are characteristic of the latter. *Quercus Robur* (=*Q. pedunculata*) occurs in both, but not as a dominant tree. *Caltha palustris*, *Spiræa Ulmaria*, *Iris Pseudacorus*, and *Carex paludosa* are abundant in the fringing carrs, but they seldom or never flower. The rest of the ground vegetation of both types of carr is composed of fen-inhabiting species.

Alder-willow thickets, as they are developed in other parts of the country, have not as yet been studied in any detail. Like those already referred to, they are found only on very wet soils, with the water level at or very near the surface, fringing the flat banks of slowly running streams, or round ponds and on springy ground within woods belonging to one of the other principal series. The dominant trees are the alder (*Alnus rotundifolia*), the sallows (*Salix capræa* and *S. cinerea*), the crack willow (*S. fragilis*), more rarely the white willow (*S. alba*), and the osier (*S. viminalis*). In the upland portions of the northern Pennines, *S. nigricans* and *S. phylicifolia* occur. The ash (*Fraxinus excelsior*) is also often abundant in these thickets.

The thickets are very frequently coppiced along with the drier woods of different types which often adjoin them and into which they may gradually pass. In the marshy meadows along streamsides, *i.e.*, in very much the situations of the corresponding natural associations, planted coppices of alder or ash are often met with. "Osier beds" are similar plantations on wet clayey or alluvial soils, but apparently rarely on peat.

The ground vegetation of these thickets is characteristic. The great hummocks of *Carex paniculata* are a striking feature. These occur also in the Norfolk "carrs," together with the smaller tufts of *C. paradoxa*. The tall and graceful *Carex pendula* and some others of the larger sedges are also found. *Scirpus sylvaticus, Œnanthe crocata, Cardamine flexuosa, C. amara, Caltha palustris, Mentha* spp., *Epilobium hirsutum, Nasturtium officinale, Myosotis palustris, Chrysosplenium oppositifolium, Iris Pseudacorus, Valeriana sambucifolia, Scrophularia aquatica, Spiræa Ulmaria, Aira cæspitosa, Phragmites communis*, and *Molinia cærulea* are other characteristic species of this association. Rarer but equally typical are the following:—*Carex Pseudo-cyperus, Phalaris arundinacea, Calamagrostis Epigeios, C. lanceolata, Lastræa spinulosa, L. Thelypteris, Osmunda regalis*, and *Equisetum sylvaticum*.

II.—OAK AND BIRCH SERIES.

The woods of this series are found on all the "siliceous" (*i.e.*, non-calcareous) soils, ranging from the stiffest clays, through the various loams, to the sands and gravels and the soils derived from sandstones of various ages, as well as on the soils derived from the older non-calcareous rocks, such as grits, mudstones, shales, and various acidic igneous rocks.

Within the series we may distinguish (A) **Oakwood Associations**, (B) an **Oak-birch-heath association**, and (C) a **Birchwood association.**

(A). **Oakwood associations.** These are by far the most widely distributed of British woodland types, occurring as they do on the stiffest clays, on all the loams and fine-grained sandstones (whose soils when wet "puddle" like clays), and also on the coarser sands and gravels, provided they are sufficiently moist. *Quercus Robur* (=*Q. pedunculata*) is the dominant tree on these soils, but *Q. sessiliflora* may also be found on the more coarsely grained soils alternately dominant or sharing dominance with *Q. Robur.* On the siliceous shallow-soiled (dysgeogenous) palæozoic and igneous rocks of the west and north, *Q. sessiliflora* is the dominant species, to the exclusion, for the most part at least, of *Q. Robur*, except where the latter species has been planted. *Q. sessiliflora* may also be dominant on the geologically more recent sandy rocks of the south of England, especially where the soil is rendered shallow by the occurrence of a hard layer a few feet below the surface, *e.g.*, over the chert of the Hythe beds of west Kent, and over the locally massive sandstones of the Tunbridge Wells beds.

Owing to the great variety of the soils on which the oak is dominant, the associated trees, and especially the ground vegetation, of the oakwoods show a wide range. The following associations (or perhaps groups of associations) may be conveniently distinguished, their characteristic ground vegetation being related to the soils on which they occur.

(a) *Damp Oakwoods.* These occur on clays and on most of the loams (except where the soil is permanently very wet), *e.g.*, on the London Clay, the Gault, the Weald Clay, and much of the "clay with flints" covering the chalk plateaux in the south of England. *Quercus Robur*, the pedunculate oak, is always the dominant tree. Locally, as on the London Clay north of London, and on the clay in parts of the Weald of Sussex, the oak is accompanied by hornbeam (*Carpinus Betulus*) which is often abundant, and usually, but not invariably, coppiced or pollarded. In these districts, hornbeam coppice is often mixed with, and sometimes replaces, hazel coppice.

The ash (*Fraxinus excelsior*) is a common and sometimes an abundant constituent of the damp oakwood, especially on deep moist soils. Along stream sides it is frequently locally dominant, and here, with its associated ground vegetation, it may be regarded as the "tailing off" of the Alder-Willow-type of vegetation previously described. In the copsewoods of the south of England, ash is usually coppiced along with the hazel. An interesting variant of the damp oakwood is seen in parts of Westmorland, as on the steep slopes of Naddle Forest above Haweswater, where there is an annual rainfall of 50 to 80 inches. Here the ash not only follows the courses of the streams, but spreads away from them in all directions; and, helped no doubt by the high rainfall, it dominates considerable areas of the wood, almost to the exclusion of the oak. Such woods may well be termed oak-ash woods, or perhaps, since birch is also very strong in them, oak-ash-birch woods. At higher levels, they pass into birch-ash woods, and eventually into birch-woods, thus forming an altitudinal series of a "damp" type, characterised by the presence of the ash, parallel with the series of drier woods described on p. 135, *et seq.*: (see also the scheme, p. 149).

The birch (*Betula tomentosa*, more rarely *B. verrucosa*) is also a common constituent of damp oakwoods, and, like the other associated trees, is very often coppiced.

One of the most ubiquitous shrubs of the damp oakwood is the hazel (*Corylus Avellana*); and this type of wood is very frequently grown as oak-hazel copse. Indeed the great majority of the damp oakwoods of southern England are oak-hazel copses. It seems probable that they arose in the following manner. The increasing demand for timber, especially in the later Middle Ages led to very extensive felling of the dominant oaks; and the breaking of the forest canopy, which was thus brought about, led to a much increased access of light to the layer of shrubs below, and greatly stimulated their development. When the undergrowth was cut to the stumps under these new conditions, the shrubs were found to throw out vigorous coppice-shoots, which then came to be regularly harvested with a rotation of approximately ten or twelve years. A certain number of oaks were left as standard trees or allowed to grow up from the stools. Various old statutes, *e.g.*, one of Henry VIII., enacted that at least twelve "standels" were to be left to the acre. These statutes originated in the alarm felt at the great decrease in the available supply of timber, the woods frequently being coppiced wholesale to supply the immediate demands for firewood,[1] fencing and the like. The standard oaks thus left at a considerable distance apart developed the freely branching habit characteristic of this tree when grown in the open. The kind of timber yielded by such trees was particularly useful in shipbuilding because of the number of "knee-pieces" formed.[1] Modern forestry, on the other hand, aims at the production of "clean" straight timber, produced by growth of the trees in close canopy.

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[1] Particularly for charcoal in the ironstone districts of the Weald.

It is easy to see how in this way the characteristic oak-hazel copses of southern England originally came into being. Many of the existing copses are certainly on the sites of ancient oakwoods: others again have no doubt been planted *de novo*.

While hazel is usually the most abundant member of the shrub-layer, all the shrubs and trees which naturally belong to this type of wood, and which stand coppicing well, are represented in the coppice.

Oak, hazel, and the other trees and shrubs of course sowed themselves naturally in the original woods, and a certain amount of felling stimulated their natural reproduction from seed; but too drastic felling and clearing lead to deterioration of the soil in various ways, and check or even quite stop natural rejuvenation of the woodland. Constant exposure of the soil leads to the destruction of the natural humus and its characteristic woodland plant-carpet, the soil becoming closely covered with grass and other weeds, or to the surface caking hard, so that seedlings have little chance to grow; while extensive clearing of the seed-bearing trees and shrubs seriously diminishes the supply of available seed. The increase of ground game also, particularly of rabbits on the lighter soils, is a very serious factor working against natural rejuvenation. The effect of these influences has been that many of the woods are not rejuvenating themselves naturally, and have had to be planted up both with standards and coppice shrubs, to fill up serious and increasing gaps. Where this has been neglected, the vegetation has degenerated to scrub and grassland. The results of planting can often be seen in the woods; but in many cases it is almost impossible to tell, in the absence of planting-records (which are very rarely available), how far it has been practised. Where, however, the coppice is pure hazel or pure ash, for instance, we may usually infer that the modern wood largely owes its composition to the choice of the forester; while, on the other hand, where the coppice shows a great mixture of shrubs, many of which are economically useless, we may conclude that the composition of the shrub flora of the wood differs but little from the original state, though the additional illumination undoubtedly encourages the growth of the shrubs as a whole.

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[1] See for instance Nisbet, *op. cit.*, p. 91, *et. seq.*

Besides the hazel and the above-mentioned trees, the following trees and shrubs are common in damp oak woods: hawthorn (*Cratægus monogyna*), sloe (*Prunus spinosa*), holly (*Ilex Aquifolium*), various fruticose Rubi, various briers, especially *Rosa canina* and *R. arvensis*, maple (*Acer campestre*), sallows (*Salix capræa* and *S. cinerea*), aspen (*Populus tremula*), dogwood (*Cornus sanguinea*), and guelder-rose (*Viburnum Opulus*). All these are generally cut indiscriminately when coppicing takes place; but the hawthorn, sloe, holly, brambles, and briers do not of course form stools. Of climbers, ivy (*Hedera Helix*) and honeysuckle (*Lonicera Periclymenum*) are typical species. The variety of shrubs, and indeed of herbaceous species too, is much less in oakwoods than in those of the ash type.

Of herbaceous species, as of shrubs, the majority are common to all damp, shady woods, and not many species are found exclusively in damp oakwoods, *i.e.*, few are confined, or nearly confined, to damp non-calcareous soils: *Equisetum sylvaticum*, *Lastræa montana* (=*L. Oreopteris*), *L. dilatata*, *L. spinulosa*, *Athyrium Filix-fœmina*, *Carex lævigata*, *Luzula maxima*, and *Scutellaria minor* may, however, figure in this category.

Of abundant plants, which are nevertheless by no means confined to woods of the oak type, a few may be mentioned.

Among species which flower in spring, the primrose (*Primula vulgaris*) is one of the best known, most abundant, and most widely distributed. The cuckoo-flower or lady's smock (*Cardamine pratensis*) is extremely abundant in many woods of this type in Kent; and the dog's mercury (*Mercurialis perennis*), the wood spurge (*Euphorbia amygdaloides*), the greater stitchwort (*Stellaria Holostea*), the red campion (*Lychnis dioica*), the wood anemone (*Anemone nemorosa*), the lesser celandine (*Ranunculus Ficaria*), and the yellow dead-nettle (*Lamium Galeobdolon*) are other prominent, spring-flowering, social or sub-social species. The luxuriance of these is greatly encouraged by the coppicing of the shrubs, and all, either locally pure, or mixed, often cover the ground of the copses and coppices in continuous sheets during April and May. On the lighter soils, the bluebell (*Scilla non-scripta*) must be included in this list. To these may be added the following, less social in habit: the wood sedge (*Carex sylvatica*), the early purple orchis (*Orchis mascula*) the barren strawberry (*Potentilla sterilis*), the true strawberry (*Fragaria vesca*), the wood sorrel (*Oxalis Acetosella*), the ubiquitous wood violet (*Viola Riviniana*), and the wood sanicle

(*Sanicula europæa*). Of later flowering species, there are the wood grasses, *Brachypodium sylvaticum*, *Melica uniflora*, *Milium effusum*, *Bromus asper*, and *Festuca gigantea*, the wood rushes *Luzula maxima* and *L. vernalis*, the wood dock (*Rumex viridis*), herb-robert (*Geranium Robertianum*), the bush vetch (*Vicia sepium*), the common willow-herb (*Epilobium montanum*), the wood loose-strife (*Lysimachia nemorum*), and the less common moneywort (*L. Nummularia*). To these may be added meadow-sweet (*Spiræa Ulmaria*), the wood avens or herb-bennet (*Geum urbanum*), *Angelica sylvestris*, bugle (*Ajuga reptans*), wood betony (*Stachys Betonica*), self-heal (*Prunella vulgaris*), great valerian (*Valeriana sambucifolia*), the devil's bit scabious (*Scabiosa Succisa*), burdock (*Arctium* spp.), and *Cnicus palustris*. Of ferns, the male fern (*Lastræa Filix-mas*) is on the whole the commonest; indeed it is the only fern at all abundant in the woods of southern and eastern England, with the exception of the bracken (*Pteris aquilina*), which is confined to those woods of the damp type which have a fairly light loamy soil; but in these it is locally extremely abundant. In the west and north of England, several other ferns are abundant, no doubt in consequence of the damper and milder climate. These include the lady fern (*Athyrium Filix-fœmina*), the broad buckler fern (*Lastræa dilatata*), with the closely allied *L. spinulosa*, and the sweet mountain fern (*L. montana*=*L. Oreopteris*).

Some of the oakwoods with a very wet surface soil, as in north Wales and in parts of Ireland, have a ground flora in which mosses are dominant, *e.g.*, species of *Hypnum*, *Dicranum*, *Mnium*, *Atrichum undulatum*, with local societies of bog-moss (*Sphagnum*) and such species of wet soil as the Marsh Violet (*Viola palustris*). A peaty soil tends to accumulate in woods of this type, and sometimes such peat-loving plants as the Bilberry (*Vaccinium Myrtillus*) become dominant. These woods have not yet been thoroughly studied, but it seems likely that they bear somewhat the same relation to moorland vegetation as the dry oakwoods, in which a heathy flora is increasing, bear to typical heath vegetation (see pp. 131-135).

The damp oakwoods are connected by every gradation with dry oakwoods, as the soils vary through the lighter loams and the finer sands to the more coarsely grained sandstones, grits, etc. As has already been pointed out, however, a very damp climate may counteract the effect of more coarsely grained soil and thus lead to the occurrence of the damp oakwood communities on these soils of coarser texture.

(b). *Dry oakwoods.* These occur on the drier "siliceous" soils above mentioned. The dominant trees are either the pedunculate oak (*Quercus Robur*), or the sessile-fruited oak (*Q. sessiliflora*), which is especially dominant on shallow-soiled rocks, or finally a mixture of the two. Where the last condition occurs, hybrids between the two species are invariably to be found.[1]

As contrasted with the oakwoods on damp soils, the typical dry oakwoods are characterised by an absence of ash, a scarcity or absence of hazel (except apparently where planted), and an absence also of such shrubs as maple, sallow, dogwood, and guelder-rose. The birches, on the other hand, are characteristically strong (mainly *Betula tomentosa*, but also *B. verrucosa* and hybrids), and so is holly; while in south-eastern England, beech is also commonly present, and is locally developed in pure societies, as on the Barton Sands of the New Forest, on the Lower Greensand of Kent and Surrey, etc.

In the hop districts of Kent, sweet chestnut (*Castanea sativa*) is frequently met with on these soils in the form of pure coppice, *e.g.*, on the Lower Greensand and on the Tunbridge Wells Sands, the last named geological formation bearing both damp and dry oakwoods, according to its local variations. The deep shade of chestnut coppice renders the soil beneath practically bare of vegetation, and the quickly drying surface forms an unsuitable *nidus* for vegetation even after the coppice has been cut.

The soil of the dry oakwood is characteristically poorer in humus than that of the damp type; and the herbaceous flora as well as the shrubby flora is much poorer in species.

The primrose and other species which flourish on clays and loams are scarce or absent. Three of the most typical dominant ground species are the bracken (*Pteris aquilina*), the wood soft-grass (*Holcus mollis*), and the bluebell (*Scilla non-scripta*).[2] The bracken and the bluebell also occur, as has been said, on the lighter loams of the damp oakwood type.

Of other species characteristic of the dry woods, we may mention the wood sage (*Teucrium Scorodonia*), the tormentil (*Potentilla erecta*), the sheep's sorrel (*Rumex Acetosella*), the wood anemone (*Anemone nemorosa*), the upright St. John's wort (*Hypericum pulchrum*), the foxglove (*Digitalis purpurea*), the rock bedstraw

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[1] See Moss, "British Oaks"; *Journ. of Bot.*, Jan. and Feb., 1910.

[2] See T. W. Woodhead, Ecology of Woodland Plants in the Neighbourhood of Huddersfield. Journ. Linn. Soc. Bot., Vol. XXXVII., 1906, p. 333.

(*Galium saxatile*), the golden-rod (*Solidago Virgaurea*), and the hawkweeds, such as forms of *Hieracium vulgatum* and *H. boreale*.

(B). **Oak-Birch-Heath association.** In the dry oakwoods, more or less isolated patches of heath vegetation are often found, with the bilberry (*Vaccinium Myrtillus*), the characteristic heath grass, *Aira flexuosa*, and in well lighted spots, the ling or heather (*Calluna vulgaris*). Sometimes considerable areas, or the whole of the woodland floor, are covered with this heath vegetation, and thus we pass to woods of the oak-birch-heath association, a very common type on the light sandy soils of south-eastern England and very sharply contrasted with all other kinds of woodland in this region. Wide areas are covered with this type of wood in Kent, Surrey and Sussex, and are continued locally and intermittently so far north as Cheshire (*e.g.*, in parts of Delamere Forest) and the Bunter Sandstone of Nottinghamshire (*e.g.*, in parts of Sherwood Forest). The association is confined to the coarser sandy and gravelly soils.

The typical native trees are oaks, either *Q. Robur* or both *Q. Robur* and *Q. sessiliflora* with hybrids, or, more rarely, *Q. sessiliflora* alone. Birches (chiefly *Betula tomentosa*, but *B. verrucosa* and hybrids also occur) are often very abundant and even dominant locally; and, in southern England at least, the beech (*Fagus sylvatica*) occurs more or less commonly, sometimes forming local woods where the deep shade cast by this tree excludes almost all competition and greatly impoverishes the ground-vegetation. Hazel, and many other shrubs, are typically absent from this kind of woodland. The characteristic shrubs and small trees are holly (*Ilex Aquifolium*), mountain ash (*Pyrus Aucuparia*), hawthorn (*Cratægus monogyna*), and blackthorn (*Prunus spinosa*). The "alder buckthorn" (*Rhamnus Frangula*), sometimes the juniper (*Juniperus communis*), the yew (*Taxus baccata*) and the whitebeam (*Pyrus Aria*), are also characteristic of many such woods, the last three being better known as plants of calcareous soils. The ubiquitous climber, honeysuckle, (*Lonicera Periclymenum*) is also found. Of planted trees, the Scots pine (*Pinus sylvestris*) generally and abundantly, and the sweet chestnut (*Castanea sativa*) and the Turkey oak (*Quercus Cerris*) occasionally, spring up from self-sown seed.

The ground-vegetation, as the name of the association implies, consists of typical heath plants. The ling (*Calluna vulgaris*) is frequently dominant where the illumination is sufficient; associated with this, and locally dominant we have the purple heath (*Erica *cinerea*). *Pteris aquilina* and *Vaccinium Myrtillus*, both of which can tolerate fairly deep shade, may be dominant both under trees and in the open. *Aira flexuosa* is the characteristic grass; while *Teucrium Scorodonia*, *Galium saxatile*, *Potentilla erecta*, and, in locally damp places, *Molinia cœrulea*, *Erica Tetralix*, and *Salix repens* occur.

The oak-birch-heath association gives a much more open and less shady wood than the typical oakwoods, except where beech is locally dominant, in which case quite the opposite condition obtains. The foliage of the birches allows more light to pass to the ground than does that of the oaks; and the trees are often separated by considerable intervals, in which the heath-plants have the ground to themselves. In this case, there are frequently wide stretches of pure heath without trees, or with only isolated trees or shrubs (*e.g.*, birch or hawthorn), in the intervals of the woodland. Many extensive areas of sandy soil, as is well-known, bear no woodland at all, but are covered entirely by heath-vegetation.

It is indeed a question whether the oak-birch-heath association is not always, as it certainly is often, a stage in the degeneration of oak forest to heathland. Graebner[1] came to the conclusion that the majority of the great heaths of the north-west German plain, which are floristically and ecologically closely akin to our own south-eastern heaths, occupy the positions of ancient woodland that naturally degenerated and finally disappeared before the invading heath-plants. Graebner believes he has established the occurrence of a continuous natural process at work on the woodlands of light soils where there is a rainfall of 70 cm. (28 inches) or more. According to him, under such conditions, the surface layers are being continually impoverished in mineral salts by washing out or "leaching," and the typical plants of the forest-floor are thus starved and give way before the invasion of mosses and shade-bearing heath plants. The matting together of the surface-layers of soil by the rhizoids and rootlets of the invaders prevents the access of oxygen to the soil, and leads to the accumulation of "acid humus" or "dry peat" (Rohhumus) in place of the original "mild humus" of the woodland soil. Thus we have the formation of a type of wood with a heathy vegetation, poor in species, on a soil composed of a mixture of sand and dry acid humus or peat. Finally, according to Graebner, either by the leaching of the soil to such a depth that the roots of the trees can no longer obtain enough food, or by the formation below the surface of a layer of "Ortstein" (moor pan), *i.e.*, a hard layer of sand bound together by humous compounds, which the roots of the trees cannot penetrate, the rejuvenation of the wood is rendered impossible, the gaps formed by the dying of the old trees are not filled up, and the forest is eventually replaced by heath.

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[1] Die Heide Norddeutschlands, Leipsig, 1901.

Whether all the steps of such a natural process unassisted by human activity have actually occurred in this country has not yet been ascertained: the subject needs a great deal more investigation. It is certain, however, as Graebner admits,[1] that the process of replacement of woodland by heath is at any rate much accelerated by extensive felling of trees; this, as was explained earlier in the present paper, leads to rapid deterioration of the soil through destruction of the mild humus by sun and wind, and, on suitable soils, enables certain mosses and other plants of the heath-association to find an entry. Not only does the felling of mature trees considerably diminish the supply of seed, but there can be no doubt that the occupation of the soil by a heath-vegetation with its accompanying layer of acid peat checks, or altogether arrests, its recolonisation by such a tree as the oak. This is perhaps partly due to unfavourable conditions for germination. The growth of seedlings is also severely handicapped by the enormous multiplication of rabbits, that especially affect the light sandy soils in which they can easily burrow. The actual stages of degeneration of woodland on sandy soils through such factors as these can be readily observed in scores of places in the south of England; and there is little doubt that many of the heaths of this region were at one time covered with forest. Whether they were all so covered is another question. Some southern heaths are certainly very old, as we know from old descriptions and place-names; but if a natural process of forest degeneration by the leaching of the surface soil has been going on since the close of the Glacial Period, it may be that heath had in some cases replaced forest by the beginning of the historical age. It is also a possibility that some soils were primitively colonised by heath-plants, and not by trees, owing to the extreme poverty of the soil. Perhaps this is true of the East Anglian heaths, as it is of some of our fixed littoral sand-dunes; but the problem has not yet been investigated.

Though the oak, from whatever cause, certainly finds a difficulty in recolonising our heaths, the birch is much more successful. This is no doubt largely due to the abundance of the seed, and to its efficient dispersal by wind, partly to the well known fact that the birch succeeds better on poorer soil than the oak. Partly owing to this cause, and partly, perhaps, because birch yields timber of much less value, and was therefore largely left during the period of great demand on oak for the navy, the native woodland of sandy soils is now very largely, and over some tracts almost exclusively, birch. This is the case for instance in Worth Forest, on the Hastings Sand of Sussex.

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[1] Graebner, loc. cit., p. 64.

A new factor in the vegetation of these sandy soils was introduced by the extensive planting of Scots pine (*Pinus sylvestris*), which, according to most authorities, is not native in southern England.[1] This tree is said to have been introduced into the New Forest about 1770, but some of the southern planting probably dates back a good deal earlier than that. On all the dry sandy and gravelly soils, Scots pine flourishes exceedingly and reproduces itself freely from self-sown seed. In the neighbourhood of old pine plantations or of mature self-sown woods, thousands of pine seedlings in all stages of growth may be found colonising the heathlands, and, to a somewhat less extent, the open oak-birch woodlands. In this way, many of the south English heaths are being rapidly converted into pine woods, the pine easily beating the oak and beech in facility of seed-distribution, while the deeper shade which it casts enables it to conquer the birch in the later stages of competition. The process is only checked by the frequent heath and forest fires which occur in this part of the country in dry summers. On the wetter soils of the hills of the north and west of England, pine does not now spread naturally to any appreciable extent,[2] though in the region of the Pennines, there is evidence from the wood found beneath the peat that pine formerly occurred as an occasional constituent of the ancient woods.

Thus we see that much of the oak-birch-heath woodland is almost certainly derived from the dry type of oakwood and represents a stage of its degradation to heath, while some may perhaps be in a "static" phase, representing a compromise between the soil-conditions favourable to the existence of close forest and those favourable to the existence of heathland. In any case, it represents an extremely well-defined and easily recognisable type of vegetation, with constant and characteristic soil-conditions and flora; and this in spite of its locally and widely varying features, consisting here of a mixed open wood of oak, birch, beech, and pine, there of pure beech high forest, and in other places of pure pinewood or of pure heath.

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[1] It is, however, at least possible that the Scots pine is a native constituent of our southern woods. There are several records of the occurrence of pine wood in the southern peat, and it may be that the tree has remained as a subordinate constituent of the dry oakwoods till extensive clearing afforded the conditions for rapid colonisation of the sandy soils.

[2] On the Cleveland moors of north-east Yorkshire, however, where the rainfall is relatively low, the Scots pine spreads freely from seed.

(C). **Birchwood association.** In the hilly districts of the north of England, the oak (*Quercus sessiliflora*) becomes rare at altitudes above 1,000 feet, whereas the birch (*Betula tomentosa*) ascends to 1,500 feet. It seems incontestable that this is due to climatic influences, as in all northern countries where the two trees occur the birch attains higher altitudes and higher latitudes than the oak. If, in the north of England, a well-wooded hill composed of non-calcareous rocks is ascended, woods dominated by the oak (*Q. sessiliflora*) are at first met with; but, as the altitude increases, the oaks gradually diminish in number and size. The diminution in number of the oaks is attended by an increase in number of the birches; until, at altitudes above 1,000 feet, a wood dominated by the latter trees is entered. Along with the oak, most of the other trees and shrubs of the oakwoods are left behind when the higher altitudes are reached; and similarly the number of ground species becomes much smaller. Since no Alpine and very few sub-Alpine species take the place of the lowland species, the floristic features separating the birchwoods from the oakwoods of the north of England, are largely of a negative character. Ecologically there are positive differences, as there is a rearrangement of the dominant members of the two associations. They are connected by all possible gradations, and the general soil conditions are identical. A birchwood in fact is simply a wood in which the oaks, on account of the increased exposure consequent on the increased altitude, have largely or entirely disappeared, and in which the birches have profited by the absence of the competition of the oaks, just as they do when the oaks have been extensively cleared in the oak-birch-heath association previously described.

Among the small trees and the shrubs of the birchwoods, the mountain ash (*Pyrus Aucuparia*) is often conspicuous; while hawthorn

(*Cratægus monogyna*) and sallows (*Salix capræa* and *S. cinerea*) are often abundant. Holly (*Ilex Aquifolium*) occurs, but rarely flowers or fruits. Upland forms of Rosa and Rubus are found, and are sometimes abundant; while ivy (*Hedera Helix*) and honeysuckle (*Lonicera Periclymenum*) are locally very plentiful.

The ground-vegetation resembles either that of the adjoining grasslands or of the adjoining moorlands. In the former case, heath-loving grasses such as *Aira flexuosa* form a springy turf. Scattered among the grasses are *Galium saxatile*, *Carex binervis*, *C. pilulifera*, *Potentilla erecta*, and upland Bryophytes. The bracken (*Pteris aquilina*) sometimes occurs in extensive sheets, and at other places is less abundant or even quite absent. In the woods with a ground vegetation made up of moorland under-shrubs, which often almost entirely clothe the ground, heather (*Calluna vulgaris*) and bilberry (*Vaccinium Myrtillus*) are the most abundant and characteristic species. The relative frequency of the two species is determined to some extent by the shade cast by the leaves of the shrubs and trees overhead; for the bilberry invariably penetrates into more shady portions of the wood than the ling or heather. Locally, the cowberry (*Vaccinium Vitis-Idæa*) is abundant, and *Molinia cærulea* occurs amongst the under-shrubs. Mosses and liverworts are abundant, especially *Sphagnum* spp., *Polytrichum commune*, *Campylopus flexuosus*, *Dicranum scoparium*, *Aulacomnium palustre*, *Webera nutans*, *Hypnum* spp., *Lepidozia reptans*, and *Nardia scalaris*.

It will be seen that the ground vegetation of the upland birch woods of the north of England has much in common with that of the oak-birch-heath association of the south, but that it contains many elements indicating the damper conditions.

Several rare species of flowering plants which are found in the old birchwoods and pinewoods of Scotland fail to reach so far south as northern England. *Corallorhiza trifida* stops at the Border: *Goodyera repens* practically stops in Cumberland, but has outlying stations in east Yorkshire and Norfolk: *Linnæa borealis* and *Pyrola secunda* are rare in northern England; while *P. uniflora* is unknown there. *Listera cordata* and *Trientalis europæa*, which occur in the Scottish birchwoods, exist on the Pennines as moorland plants only; and even on the moors, they are rare and local. *Pyrola media* and *P. minor* appear, in fact, to be the only species of this class which are typical both of the Scottish birchwoods and of those south of the Border country; and even these species are rare and local throughout the whole of England.

Judging from the timber which is sometimes found buried under the peat of the Pennines, it seems to be the case that the Scots pine (*Pinus sylvestris*) formerly occurred in the birchwoods of the north of England; but as pine timber under the peat of this region is only seldom met with, and as birch timber is abundant in such situations, it seems equally clear that the primeval woods were dominated by the birch, and that the pine was never more than a local, or at most a locally abundant member of the prehistoric woods of the hills of northern England. While the present birch woods on the Pennines only ascend to about 1,250 feet, and even birch scrub only reaches about 1,500 feet, the buried birch stems indicate that formerly this tree reached an altitude of between 1,700 and 1,800 feet.

In the recent plantations on these hills, seedlings of pine from self-sown seeds, though they do occur, are not numerous; and the species therefore does not seem to thrive here as it does on the drier heaths of southern and eastern England and of north-east Yorkshire.

In central Scotland, woods dominated by the Scots pine occur; but they have not been examined ecologically, though Robert Smith has briefly described some primitive woods of birch and pine in Perthshire.[1]

III.—BEECH AND ASH SERIES.

The woods of this series are found on calcareous soils, such as marl, chalk and limestone, where the lime-content of the soil is high.

Within the series we may distinguish (A) an **Ash-oakwood association** (B) an **Ashwood association** and (C) a **Beechwood association.**

(A) and (B) are the characteristic woodland types on all highly calcareous soils except those of the south-east of England, where the beech is dominant on the Chalk, beating the ash in competition owing to the much deeper shade which it casts. In parts of this district, however, the ash is important as a potential wood-former; and, as on the Chalk of south-east Hampshire, ashwoods may be developed side by side with beechwoods, perhaps owing to extensive clearing of the latter. In the Isle of Wight, the beech does not appear to form natural woods; and there the calcareous soils of of the Chalk bear well-developed ashwoods. Westwards from Hampshire, through Dorset to the western limit of the Chalk in east Devon, ashwoods occur on the calcareous soils of the Chalk and Upper Greensand.

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[1] Botanical Survey of North Perthshire, Scottish Geogr. Mag., 1901.

The area of natural or semi-natural beechwoods appears to have a western extension on the Inferior Oolite of the Cotswolds, but for the most part it does not extend north-westward of the Chalk escarpment.

(A). **Ash-oakwood association.** This association is allied to that of the damp oakwood, into which it sometimes passes imperceptibly, thus forming a link between the two chief woodland series (see Scheme, p. 149). It occurs on highly calcareous clays, such as the Boulder clay of Cambridgeshire and neighbouring counties, on the Jurassic marls of Somerset, on the highly calcareous Upper Greensand of Hants, Dorset and East Devon, on some of the Silurian limestones of Herefordshire and district, on the deeper-soiled tracts of Mountain or Carboniferous Limestone, and on the calcareous glacial drift of the southern fringe of the Lake District.

The ash and the oak share dominance in these woods so far as they are not coppiced, and the two are present in very various proportions in different woods. While *Quercus Robur* is the only oak in woods of this type on the calcareous marls and clays of the south, *Q. sessiliflora*, either alone or mixed with a varying amount of *Q. Robur*, is the oak of the woods referred to on the Silurian and Carboniferous Limestones.

The general ecological conditions are in many ways the same as those of the damp oakwood, and the vegetation appears, on a preliminary inspection, to be identical. But the ash-oakwood possesses in abundance a number of species characteristic of calcareous soils, which are either only occasional in, or are quite absent from the damp oakwood. It is true of the ash series generally that the woods have a greater richness of flora ; and while in the case of the woods of the oak and birch series, the great bulk of the vegetation is made up of comparatively few species, in those of the ash series it is composed of a much greater variety. Thus among shrubs, the wayfaring tree (*Viburnum Lantana*), the spindle-tree (*Euonymus europæus*), and the climbing traveller's joy (*Clematis Vitalba*) are common, while they are very rare in oak woods. Such species as the dogwood (*Cornus sanguinea*), the privet (*Ligustrum vulgare*), the maple (*Acer campestre*), and even the sloe (*Prunus spinosa*) and the hawthorn (*Cratægus monogyna*), while more or less common in oak woods, are much more abundant in those of the ash-oak association, and form a considerably greater proportion of the whole shrub-layer. The same is true of the herbaceous species. The general list is mainly the same as that of the damp oakwood; but such plants as *Carex digitata*, *Paris quadrifolia*, *Colchicum autumnale*, *Iris fœtidissima*, *Helleborine media*, *H. purpurata*, *Viola Reichenbachiana*, *Primula elatior* (an East Anglian species) *Lithospermum purpureo-cœruleum* (a south-western form), and *Campanula Trachelium*, which are almost or quite absent from woods of the oak type, are characteristic of the ash-oak association. Dog's mercury (*Mercurialis perennis*) is much more generally dominant in the ground-vegetation, and other species such as *Hypericum hirsutum*, *Vicia sylvatica*, *Aquilegia vulgaris*, *Rubus saxatilis*, *Campanula latifolia*, *Carduus heterophyllus*, and *Myosotis sylvatica* are more generally abundant.

While some ash-oakwoods (*e.g.*, many of those on the Upper Greensand of East Devon and of the Isle of Wight) are left in an almost natural condition, felling and cutting of the undergrowth being far from heavy and planting quite occasional and sporadic, the great majority of the ash-oakwoods of the southern half of England are treated as copse with standard oaks, hazel occupying much the same position as it has in the damp oakwoods. In such copses, the ash and practically all the trees except the oak, as well as all the shrubs, are cut promiscuously when coppicing takes place; and the result is copsewood of the oak-hazel type with a great variety and abundance of shrubs in addition to hazel. Such copsewoods are naturally indistinguishable by superficial observation from the oak-hazel copses belonging to the damp oak-association.

Another factor tending to the assimilation of these two associations is the frequent poverty in lime of the surface soil to a depth of some inches, probably due to leaching. This, with the accumulation of humus, leads to the establishment on the floor of the wood of shallow-rooting plants not found on soils rich in lime. The more deeply rooting plants, such as the shrubs, are often, therefore, a better index than the herbaceous species of the essentia character of these woods.

(B). **Ashwood association.** In the ash series pure ashwoods appear to bear somewhat the same altitudinal and edaphic relation to ash-oak woods that woods of *Quercus sessiliflora* bear to the damp woods of *Q. Robur* in the oak series; for just as damp woods of *Q. Robur* occur on damp, lowland, clayey and loamy soils, and woods of *Q. sessiliflora* on upland and shallow, siliceous soils, so ash-oak woods tend to occur on damp, lowland, marly soils and pure ash woods on hilly, shallow, calcareous soils. In Somerset, many of the woods, *e.g.*, Cheddar Wood, on the lower slopes of the Mendips belong to the ash-oak association; while on the upper slopes of those hills, as in Ebbor Gorge, they belong to the ash association. In north Derbyshire, ashwoods free from oaks are numerous and typical on the slopes of the Carboniferous Limestone hills at altitudes up to 1,000 feet. In these woods, the ash is dominant throughout; whereas, in the woods belonging to the oak and birch series, it is abundant only in the damper situations.

It is evident that, in any given locality, the abundance of the ash is connected with one of two factors, either a high water-content or a high lime-content of the soil. The explanation of this fact is not clear; the relation of the ash to soil-factors requires experimental investigation.

The most frequent arboreal associates of the ash are the wych elm (*Ulmus montana*) and the hawthorn (*Cratægus monogyna*). The former is more abundant at the lower altitudes and in the damper situations, the latter in the drier situations at the higher altitudes. When the ash is removed or dies out in a degenerating wood, the elm or the hawthorn becomes locally dominant. Societies of aspen (*Populus tremula*) are local, and of alder rare, in the ash woods. Societies of yew (*Taxus baccata*), beech (*Fagus sylvatica*), lime (*Tilia cordata*) and whitebeam (*Pyrus Aria*) occur in ash-woods in the south-west of England; but in Derbyshire, all these trees (except the beech, which is planted) are rare, while in some of the ashwoods to the south of the Lake District, the yew and the whitebeam are almost as frequent as they are on the Chalk. From many ashwoods oaks are entirely absent.

Several shrubs which are characteristic of the ash-oakwoods become of rare or local occurrence in the upper ashwoods, and some are altogether absent. The following shrubs belong to this category:—*Clematis Vitalba*, *Enonymus europæus*, *Viburnum Lantana*, *Ligustrum vulgare*, and *Daphne Laureola.*

The ground societies of the ash association may be classified on the basis of the water content of the soil. By stream sides and in damp places of the northern ashwoods, a very rich and varied ground flora is to be found. Among the conspicuous plants of such situations, wood-garlic (*Allium ursinum*), red campion (*Lychnis* *dioica*), columbine (*Aquilegia vulgaris*), meadow-sweet (*Spiræa Ulmaria*), wood-avens (*Geum rivale*), yellow dead-nettle (*Lamium Galeobdolon*), woodruff (*Asperula odorata*), and *Valeriana Mikanii*, are frequently abundant.

In situations of ordinary dampness, extensive sheets of dog's mercury (*Mercurialis perennis*) occur; and, in certain localities, this plant and the moschatel (*Adoxa Moschatellina*) form an interesting "complementary" society.[1]

The dry parts of the ashwood are characterised by stretches of ground ivy (*Nepeta hederacea*). Taller herbs occur, especially *Hypericum hirsutum*, *Urtica dioica*, and *Teucrium Scorodonia*, forming close herbaceous thickets in summer. The last named species belongs to an interesting class which occurs in some of the drier woods of the oak and birch series, as well as in the ashwoods, but is absent from the oak-ashwoods. Locally, the lily-of-the-valley (*Convallaria majalis*) and the stone-bramble (*Rubus saxatilis*) form fairly extensive ground societies; and in these the nodding melic-grass (*Melica nutans*) sometimes occurs.

The very driest parts of the ashwood occur on the rocky knolls. Here the soil is extremely shallow, and in places the bare rock protrudes. Trees and shrubs are absent; and the absence of shade allows of the growth of saxicolous lichens and bryophytes, such ephemerals as *Draba verna* and *Saxifraga tridactylites*, and such dwarf perennials as *Sedum acre* and *Thymus Serpyllum*. Such a community does not, except in a topographical sense, belong to a woodland association at all. Screes and cliffs are also found within the ashwoods; but these in time become clothed with trees and shrubs; and it is possible, by observing several such localities, to construct a series of plant associations which illustrate a historical natural succession from the bare screes or cliffs to the ashwood.

Ground societies of *Aira flexuosa*, *Holcus mollis*, and *Vaccinium Myrtillus*, so characteristic of the oak and birch series, are totally absent from woods of the beech and ash series.

The following species are confined to the more northern woods, and are either found only in ashwoods or are more abundant in them than in oakwoods:—*Melica nutans*, *Festuca sylvatica*, *Hordeum sylvaticum*, *Carex ornithopoda*, *Helleborine atro-rubens*, *Trollius europæus*, *Actæa spicata*, *Geranium sylvaticum*, *Polemonium*

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[1] See Woodhead, l.c., p. 345,

cœruleum, *Myosotis sylvatica*, *Campanula latifolia*, *Carduus heterophyllus*, *Hieracium* spp. The lady's slipper orchid (*Cypripedium Calceolus*) is extinct in Derbyshire, but it still lingers on in Yorkshire and Durham.

Ash-Birchwood.

In the limestone districts of the extreme north-west of England the woods of the ash series exhibit a considerable deviation from the type. While the differences scarcely affect the ground vegetation, the uppermost or tree-layer shows considerable modification. The ash is less abundant, and the birch (*Betula tomentosa*) more abundant than in the typical ash-association; while the sessile-fruited oak (*Quercus sessiliflora*) is also sometimes present. This is to be distinguished as the ash-birchwood, which is apparently conditioned by the climatic environment.

These ash-birchwoods are not numerous, even in this district. They are found on the precipitous slopes of the narrow limestone valleys or dales, and particularly on the face of the Pennine escarpment. This rises almost vertically some 2,000 feet above the plain and looks westwards towards the hills of the Lake District; and against it the "helm" wind, peculiar to this type of land-relief, impinges violently. The exposure to both wind and radiation is extreme, and in marked contrast with that of the sheltered valleys of the south. The highest altitude attained by the ash-birch woods is 1,250 feet, and the local annual rainfall is about 50 inches.

At the higher levels the birch (*Betula tomentosa*) is practically pure, and with it is associated the mountain ash (*Pyrus Aucuparia*). At lower levels the ash (*Fraxinus excelsior*) is abundant, accompanied, as in the typical ash-association, by the wych elm (*Ulmus montana*) and by *Quercus sessiliflora*. When such a wood is viewed in mass, the stout grey branches of the ash stand out prominently against the delicate brown tracery of the branches of the birch.

Of shrubs, the hazel (*Corylus Avellana*) is extremely abundant; the sallow (*Salix caprœa*), the holly (*Ilex Aquifolium*) and the hawthorn (*Cratægus monogyna*) are frequent; while the whitebeam (*Pyrus Aria*), spindle tree (*Euonymus europæus*), buckthorn (*Rhamnus catharticus*), dogwood (*Cornus sanguinea*), and yew (*Taxus baccata*) are absent except in South Lonsdale. It will be noticed that in their place are associates typical of the oakwoods.

The ground vegetation of the ash-birch woods is of the same type as that of the ashwoods, though less luxuriant; and this again is doubtless owing to the more severe climatic conditions.

Thus, this association shows some relationship with the upper hill woods of the oak and birch series, in fact a convergence with the birchwood associations of that series, namely those woods representing the extreme conditions of altitude on siliceous soils; just as, at the other end of the scale there is a relationship between the oakwoods of the non-calcareous clays and the ash-oakwoods of the calcareous marls.

(C). Beechwood Association.

Beechwoods are the characteristic woodland type of the chalk escarpments and valley sides of south-eastern England, *i.e.*, whereever the chalk forms the actual subsoil. In these situations they are found fringing the Weald on the north, west and south, *i.e.*, through Kent, Surrey, Hampshire and Sussex. They are, however, absent from the extreme eastern end of the North Downs west of Dover to about Wye, and also from the eastern end of the South Downs, westward from Beachy Head, a tract of country singularly bare of trees. From Lewes westwards to Steyning a few scattered remains of beechwood occur here and there on the escarpment. Beyond Steyning they increase considerably, while in the neighbourhood of Arundel and westwards to the Hampshire border are some of the finest beech woods in England.

On the Chalk-outcrop, which runs in a generally north-east and south-west direction through the greater part of England, the finest development of beechwoods is on the Chiltern Hills of south Buckinghamshire and east Oxfordshire, and on the chalk slopes on either side of the Thames valley. From this centre, they thin out pretty rapidly both to the north-east and to the south-west, so that in Cambridgeshire and Wiltshire respectively, they are represented only by scattered patches, many of which are clearly plantations on grass or arable land with none of the characteristic plants of the beech association.

The fine beechwoods of the Cotswolds are apparently a westward extension of the Thames valley area.

Of the causes of this circumscription of natural or semi-natural beechwood, we know very little. It seems likely that beech is speaking geologically, a comparatively recent migrant into this country from the Continent. Such a view is supported by its sub-fossil occurrence in Denmark in the recent but not in the older peat. Whether the beech be a comparatively recent immigrant or not, it seems that only in the south-east of England has it found climatic conditions enabling it to become dominant and to form woods, beating the ash, its light-demanding competitor on calcareous soils, by reason of the deep shade which it casts. While the beech has every appearance of being native so far west as Cornwall, and while it flourishes and ripens seed so far north as Scotland, where it is often successfully planted on very various soils, it appears quite unable to form natural woods outside the area indicated.[1] It may however have had its distribution as a wood-former somewhat curtailed by clearance of forest on the outskirts of its present area, *i.e.*, on the chalk escarpment on either side of the Chiltern region, for in Cambridgeshire and Wiltshire indications of natural beechwoods are not wanting.

Even within the present region of dominance of the beech, there are signs of failure in the power of natural rejuvenation by self-sown seed, though in other places such rejuvenation is still vigorously proceeding. It is certain that one very powerful factor is the multiplication of rabbits, which eat off the seedlings and do as much harm to the beechwoods as they do to the oakwoods. And just as birch and pine tend to replace oak on sandy soils when the original oakwood is handicapped by heavy clearing and the attacks of rabbits, so ash, in some places at least, seems to replace beech on the Chalk, when the beechwoods are similarly handicapped.

For the most part, beechwood stops sharply at the edge of the shallow chalk soil. Thus, for instance, the chalk plateau of the North Downs is nearly everywhere covered by the so-called "clay-with-flints," really consisting of varying clays and loams which are marked by great poverty in lime. These soils nearly always extend to the edge, sometimes over the edge, of the escarpment, but invariably stop short of the steepest slope of the latter. The "clay-with-flints" bears oakwood of the damp or of the dry type; and the transition from this to the beechwood of the escarpment or valley-side is very sudden, and corresponds very exactly with the change of soil. On the plateau of the South Downs and on the rolling chalk plain of central Hampshire, there is a good deal of oakwood on soil which is shown on the Drift maps of the Geological Survey as Chalk; but such woods are invariably found to be developed not on the chalk itself but on a non-calcareous soil overlying the chalk. On the other hand the plateau of the Chilterns, similarly covered with non-calcareous clays and loams, is often occupied by beech, or by beech and oak mixed, though sometimes, as in the cases above described, it bears typical oakwood.

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[1] It is interesting to notice that the distribution of certain associations of land molluscs, which show Continental affinities, is limited in a similar way. *Helix obvoluta*, the most typical species of these associations is found nowhere beyond the limits of the beech-association.

The beech is not only the dominant tree in the beech association; it typically forms an almost pure high forest of beech in close canopy. Occasionally an ash is met with, occasionally a white beam tree (*Pyrus Aria*), hardly ever an oak. The yew (*Taxus baccata*) is found in many beechwoods forming a distinct layer below the crowns of the dominant trees. There are practically no shrubs in a normal beechwood, the light penetrating the canopy being insufficient for their growth; but on the outskirts of the wood there is frequently a rich and varied scrub of such species as *Cratægus monogyna*, *Pyrus Aria*, *Viburnum Lantana*, *Rhamnus catharticus*, *Cornus sanguinea*, *Euonymus europæus*, *Prunus spinosa*, *Corylus Avellana*, *Acer campestre*, *Sambucus nigra*, *Juniperus communis*, and *Taxus baccata*, with the climber *Clematis Vitalba*. These species will be recognised as characteristic shrubs of the ashwood associations; and with them may often be found much ash, which sometimes grows up to form a regular ashwood with its varied undergrowth.

Under the close canopy of the beechwood itself, the shade is typically so deep as to exclude all ground vegetation except certain saprophytes; but in more open spots *Mercurialis perennis* becomes generally dominant, while *Sanicula europæa*, *Viola Riviniana* and *V. Reichenbachiana*, *Fragaria vesca*, and *Circæa lutetiana* are locally dominant. *Viola hirta* is abundant and charcteristic. The orchids *Cephalanthera pallens* and *Helleborine violacea* are also characteristic, while in the deeper humus the colourless saprophytes, *Monotropa Hypopitys* and *Neottia Nidus-avis*, are frequent, even in the deepest shade. *Atropa Belladonna*, *Daphne Laureola*, *Ruscus aculeatus*, and more rarely, *Helleborus viridis* are characteristic of more open spots on the outskirts of beech woods.

The following is a summary of the types of woodland distinguished in the present paper:—

I.—ALDER-WILLOW SERIES: on very wet soils; consisting of at least two distinct associations, as yet insufficiently studied to allow of satisfactory separation and characterisation.

II.—OAK AND BIRCH SERIES: on non-calcareous soils.

(A). **Oakwood associations**: on non-peaty soils at low and moderate elevations.

- (a). *Damp Oakwoods*: on clays, shales, loams, fine sands and moist soils generally.
  - [Derived artificial type: **Oak-hazel copse**].
    - Oak-ash-birchwoods: on shallow well-drained soils in a wet climate.
- (b). *Dry oakwoods*: on sandstones, grits, sands and dry soils generally.

(B). **Oak-birch-heath association**: on dry coarse sandy and dry peaty soils (low elevations).

(C). **Birchwood association**: on non-calcareous soils at high elevations (from 1,000 feet to the upper wood limit on the Pennines).

III.—BEECH AND ASH SERIES: on calcareous soils.

(A). **Ash-oakwood association**: on calcareous clays, marls, impure limestones. and calcareous sandstones:

[Derived artificial type: **(Ash-) Oak-hazel copse.**]

(B). **Ashwood association**: on limestones.

Ash-birchwood: on limestones at high elevations (from 1,000 feet to the upper limit of woodland).

(C). **Beechwood association**: on Chalk in the south-east of England, with a western extension on the Oolites of the Cotswold Hills.

The characters employed in the classification of English woods given in this paper are in the first place the species of dominant trees on very wet, on calcareous, and on non-calcareous soils respectively. The Oak and Birch series is then sub-divided on the basis of the nature and amount of the water-content and on the character of the humus. This method is somewhat on the lines of that used by Graebner[1] for classifying vegetation, though in the absence of sufficiently numerous accurate soil analyses, we have relied, for the present, on lime-content, rather than on the general content in soluble mineral salts which Graebner employs. The observed correlation of the second and third woodland series with lime-content is sufficiently close to afford a satisfactory basis for classification, but we have advisedly abstained from committing ourselves to the view that the lime-content is the *cause* of the observed distribution of woods. In any case we are convinced that this class of criteria furnishes a more natural basis for the primary classification of English vegetation than water-content alone, or even than so-called "physiological water-content."

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[1] Naturwissenschaftliche Wochenschrift XIII., 1898; and Die Heide Norddeutschlands, 1901, pp. 24 and 25. Also Die Pflanzenwelt Deutschlands, 1909.

We might, however, construct a classification of oakwoods on the basis of the dominant species of oak, rather than on water-content of the soil, and for such a classification there is much to be said. *Quercus sessiliflora* is certainly the characteristic oak of the north and west of England, just as *Q. Robur* is of the south and of the midlands. The vast majority of observed oakwoods are pure woods either of *Q. Robur* or of *Q. sessiliflora*; comparatively few have the two mixed. It has even been suggested that where a mixture of the two species obtains it always indicates planting of *Q. Robur*, which in the vast majority of cases, at any rate, is the species planted.[1] But we have satisfied ourselves that the mixture of the two species is too general an occurrence on certain types of soil, particularly on sands and sandy limestones, to allow of this hypothesis being entertained.

The factors which lead to the observed distribution of the two oaks are not yet clear; the two species certainly can and do flourish side by side on the same soil. Climate has been suggested as the differentiating factor, and the general distribution of the two species might seem to support such a suggestion; but it is not borne out when we consider the fact that natural or semi-natural woods of the two species occur in the same region. The most probable hypothesis is that the *main* determining factor is depth of soil, for *Q. Robur* is certainly pre-eminently characteristic of the deep-soiled clays, loams and fine sands, which are mainly found in the south, in the east and in the Midlands, while *Q. sessiliflora* is equally characteristic of the shallow-soiled palæozoic sandstones, grits and mudstones of the north and west.

If the dominant trees alone were concerned, a primary classification of oakwoods according to the dominant species would be the natural one to adopt, but a wood is a complex plant-association, and the ground-vegetation is subject to other influences than those which determine the dominant tree. Thus one may get exactly the same ground-flora in a wood of *Quercus sessiliflora* as in a wood of *Q. Robur*, because the surface soil is of the same type, though the underlying rock determines the occurrence of a different dominant.

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[1] Mr. Lascelles, Deputy-Surveyor of the New Forest, however, in a letter to one of us, states his opinion that the plantations of 1700 and thereabouts, now the finest woods of the Forest, were in many cases purposely planted with *Q. sessiliflora*.

In view of the prevailing uncertainty and confusion in the nomenclature of units of vegetation, we have avoided so far as possible the use of terms signifying units of a definite rank. The term *association* is the only term of this kind used. By an association we mean a community of plants occupying a definite habitat, with constant dominants and definite floristic composition.[1]

In the scheme on p. 149 an attempt has been made to exhibit the relations of the dominant species of tree as well as those of the conditions determining the general character of the associations.

The Alder-Willow series stands at the base, connected with both the damp lowland types, the Oak (Q.r.) and the Ash-oak (Fr. Q.r.). A vertical line divides the Beech and Ash series on the left from the Oak and Birch series on the right. The lowland types occur at the bottom, and the upland types at the top of the diagram. Various lines lead up to different examples of birch associations, the birch being the tree which is dominant at the highest altitudes. One line within the Oak and Birch series represents a series of damp woods, the moist condition being generally determined by soil in the lowland types, largely by climate in those of the uplands. To the right are the associations of acid, peaty soils, to the left those characterised by mild humus. The lines represent affinity, not necessarily genetic derivation, except where they have arrowheads.

The largest capitals are employed for the names of the great primary series; the next size of capitals is used for groups of associations and for the varied oak-birch-heath association. Medium capitals are used for the great basal associations. Small capitals for the less important associations, and italic capitals for the semi-artificial types of woodland.

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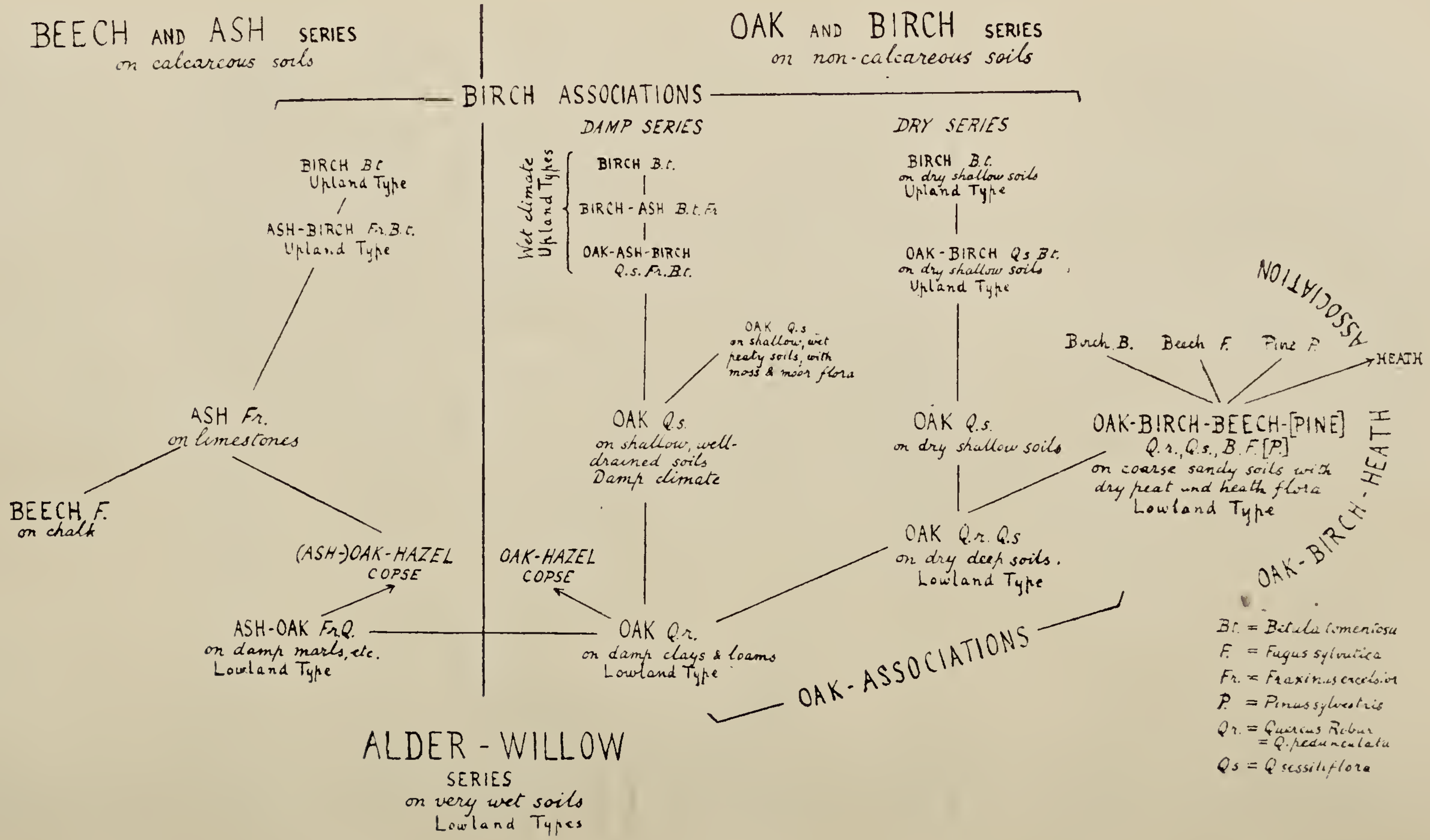
[1] For a full discussion of the concepts and nomenclature of vegetation units see Moss, "The Fundamental Units of Vegetation," New. Phyt., Vol. IX., p. 18, 1910.


BEECH AND ASH SERIES
on calcareous soils
OAK AND BIRCH SERIES
on non-calcareous soils
BIRCH ASSOCIATIONS
DAMP SERIES
DRY SERIES
BIRCH Bc
Upland Type
ASH-BIRCH Fr.B.c.
Upland Type
Wet climate
Upland Types
BIRCH B.c.
BIRCH-ASH B.c.Fr.
OAK-ASH-BIRCH
Q.s. Fr.B.c.
BIRCH B.c.
on dry shallow soils
Upland Type
OAK-BIRCH Qs Bc.
on dry shallow soils
Upland Type
OAK Q.s
on shallow, wet peaty soils, with moss & moor flora
ASH Fr.
on limestones
BEECH F.
on chalk
OAK Q.s.
on shallow, well-drained soils
Damp climate
OAK Q.s.
on dry shallow soils
Birch B.
Beech F.
Pine P.
HEATH
ASSOCIATION
OAK-BIRCH-BEECH-[PINE]
Q.r., Q.s., B. F. [P.]
on coarse sandy soils with dry peat and heath flora
Lowland Type
OAK-BIRCH-HEATH
(ASH-)OAK-HAZEL
COPSE
OAK-HAZEL
COPSE
OAK Q.r. Q.s
on dry deep soils.
Lowland Type
ASH-OAK Fr.Q.
on damp marls, etc.
Lowland Type
OAK Q.r.
on damp clays & loams
Lowland Type
OAK-ASSOCIATIONS
ALDER-WILLOW
SERIES
on very wet soils
Lowland Types
Bc. = Betula tomentosa
F. = Fagus sylvatica
Fr. = Fraxinus excelsior
P. = Pinus sylvestris
Qr. = Quercus Robur = Q. pedunculata
Qs = Q sessiliflora

NOTE ON THE ROOTS OF *TERMINALIA ARJUNA*, BEDD.

By R. S. Adamson.

[Text-Figs. 3-7.]

The material examined was collected by Mr. I. H. Burkill, near Sembadow, in the Satpura Hills of Central India, from the banks of the Sipra River, and sent by him to Professor Seward, who handed over to me for investigation.

Terminalia Arjuna Beddome is a large tree belonging to the natural order Combretaceæ,[1] and growing to a height of sixty to eighty feet. The species is confined to India and Ceylon, where it occurs commonly along the banks of streams and rivers.[2]

From the trees growing on the banks of a river, certain roots grow out horizontally into the river bed, among the stones, or just below the surface of the water. From these roots lateral branches are given off that rise vertically to the surface of the water or mud. It is such roots that I have investigated. The rivers in the district from which the material was obtained dry up during the hot season, when they are represented by a series of pools. The material was collected in October, 1908, when the level of the river was beginning to fall, and beneath all the trees of *Terminalia Arjuna* was a thick growth of the small apogeotropic roots among the stones and mud of the river bed.

In some of the deeper pools, as Mr. Burkill states in a letter, the horizontal roots bend up till they reach the surface of the water, where vertical roots are produced; they afterwards bend down again.

Structure of the Horizontal Roots.

The roots seem to be primarily triarch, though other primary strands appear later, so that older roots are hexarch to octarch. Large vessels are produced in the secondary wood, but do not occur in that formed previous to the activity of the cambium.

The medullary rays consist of a single row of cells, or are rarely two to three rows of cells in breadth; they broaden out slightly in the phloem, owing to the greater breadth of the cells in that region. The phloem consists of three kinds of cells: (i.) sieve-tubes and companion cells, (ii.) large numbers of parenchyma cells which often contain stellate groups of crystals of calcium oxalate, and (iii.) occasional fibres, either singly or in groups. The pericycle is not lignified, and the endodermis is a well-marked layer, with both radial and inner walls somewhat thickened; occasional passage cells occur.

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[1] Hooker, J. D. Flora of British India.

[2] Brandis, D. Indian Trees, 1906.

The cortical tissue is very loose with large lacunæ (Fig. 3). The individual cells are cylindric and arranged in irregularly radial rows. Beneath the epidermal layer is a hypoderm of elongated cells, polygonal in cross section, whose walls are slightly thickened.

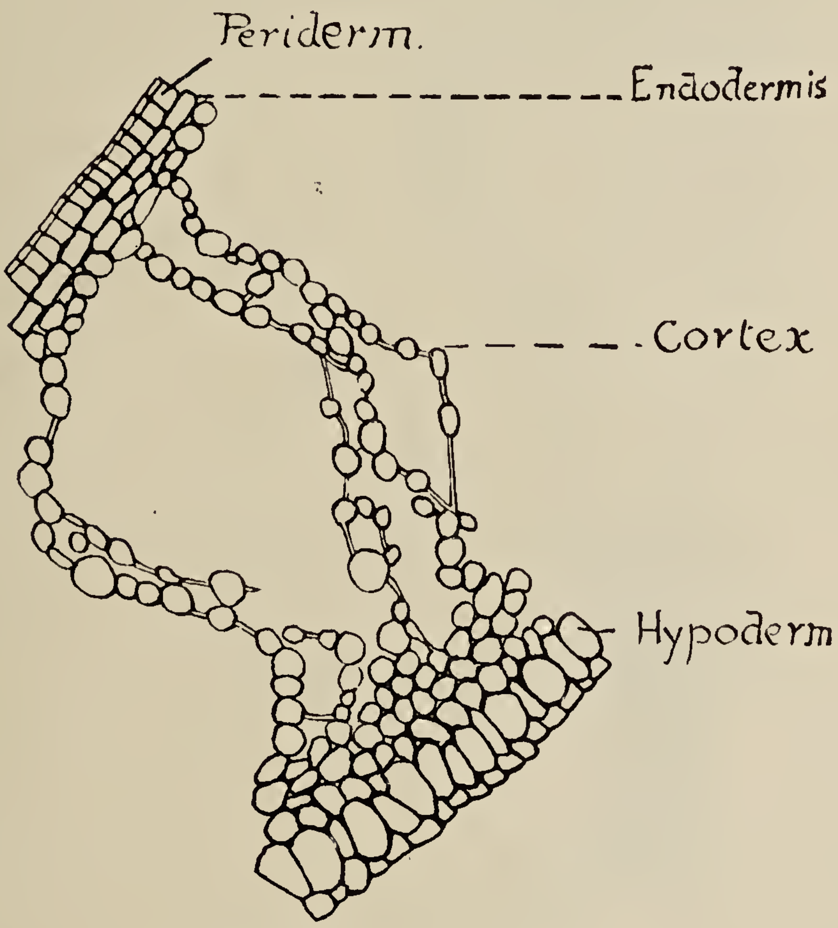

Fig. 3. Transverse section of cortical part of root.

Very soon after the beginning of secondary thickening a periderm is formed in the outer layer of the pericycle; the primary cortex is afterwards cut off. An aerating tissue forming a "secondary cortex" is then formed internal to the periderm. This is mainly derived from the secondary phloem[1] (Fig. 4). The cells of the phloem parenchyma split apart from one another, but also conjugating parenchyma is formed. In addition, some cells forming

[1] Cf. Schenk, H. Flora, 1889.

a phelloderm, are cut off internally by the phellogen, and add to this tissue. Crystals of calcium oxalate occur in some of the cortical cells, especially in the inner ones (Fig. 4).

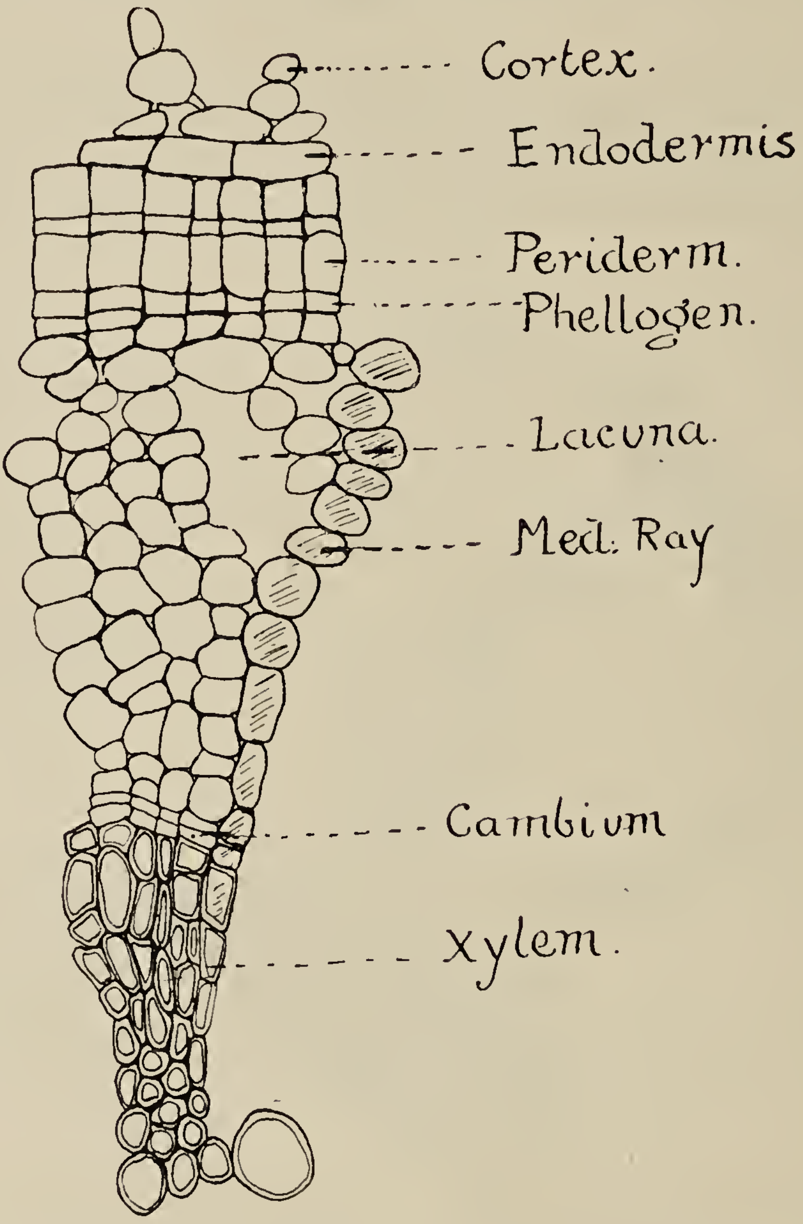

Fig. 4. Transverse section of root, showing lacunæ in secondary phloem.

Structure of the Vertical Roots.

In general structure these are very like the horizontal roots, but on a smaller scale. They differ from ordinary pneumatophores[1] in being freely branched, the branches arising endogenously in the normal manner; like the horizontal roots they are at first triarch, with additional protoxylem groups appearing later.

Near the apices of these roots the cortex is simple with a few large intercellular spaces. As the root increases in size the cortical cells grow irregularly, the result being that the cells separate from one another, but in places remain attached by lateral processes. A large lacunar system is thus formed. The connecting processes are at first produced mainly on the radial walls of the cells and to a less extent on the tangential walls, so that the cells come to be arranged in radial chains (Fig. 5). In time the processes are cut off by transverse walls. This method of growth of a lacunar system has been termed by Karsten[1] "conjugating parenchyma."[1] The process is helped by the rows of cells simply splitting away from one another.

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[1] Karsten. Bibliotheca Botanica, XXII., 1891.

A point in which the roots differ from typical pneumatophores[2] is that the root-tip is covered by a definite root-cap, though this cap is not of the normal structure seen in terrestrial roots.[3] It extends much further back than usual; the cap-cells continue as a limiting layer two to three cells deep over the region normally occupied by the root-hairs and do not finally disappear till a considerable distance behind the apex, at a point where the tissues

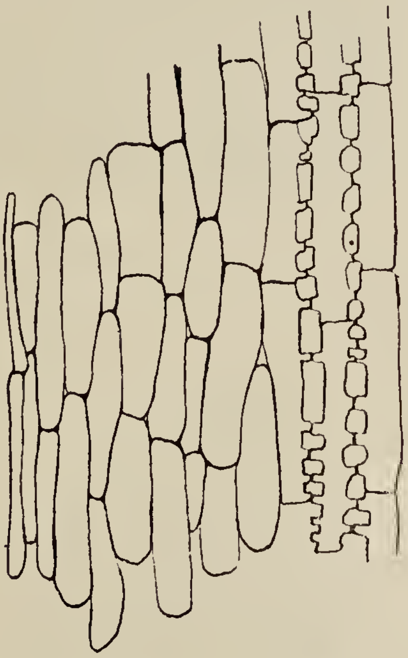

Fig. 5. Longitudinal section of cortex of a young root, showing beginning of "conjugating parenchyma."

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[1] Solcreder, Syst. Anat. Dikot, 1908.

[2] Westermaier. Zur. Kenntniss der Pneumatophoren, 1900.

[3] Janczewski. Ann. Sci. Nat., 1874.

are fully differentiated. In structure the root-cap is also remarkable (Fig. 6); it is of considerable thickness, from twenty to twenty-five layers of cells being present in some cases above the apex.

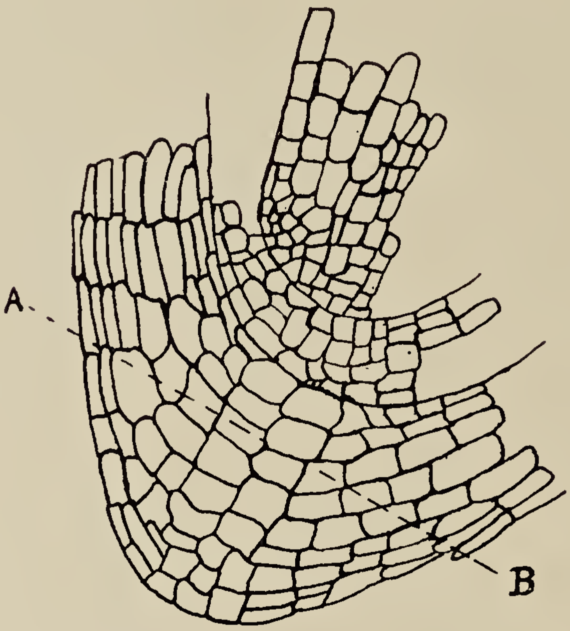

Fig. 6. Longitudinal median section of young root cap.

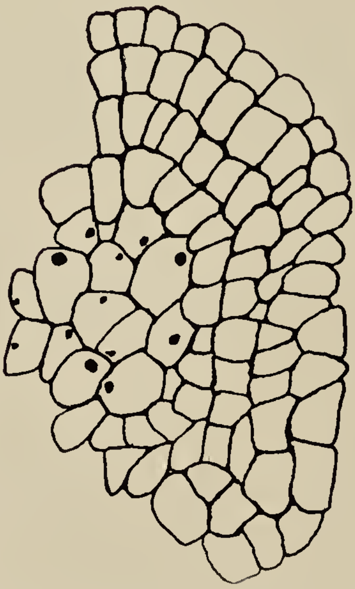

Fig. 7. Transverse section through root cap, along line A-B, in Fig. 6.

The tissue forming the cap appears to be differentiated into two parts, a central portion over the growing-point of the root (Fig. 7) and a peripheral portion (see Figs. 6 & 7). These regions are distinguished partly by the form of the cells, but more distinctly by their contents. The central core consists of large cells which are square in longitudinal section, while the others are elongated in the axial direction; intermediate stages however occur. The differentiation of contents is very sharp; the cells of the central core contain clear vacuolated protoplasm with prominent nuclei while the surrounding cells have small inconspicuous nuclei and are filled with a deeply-staining granular substance. No intercellular spaces occur between the cells of the root-cap. Root-caps of this form were found both in the horizontal and the vertical roots; in neither case are root-hairs developed at all.

Slight structural differences were noticed in roots collected from different environmental conditions: those growing wholly or partially submerged have the vascular tissues less developed, and do not form a periderm till a later period; also the hypodermal layer is less distinct, especially in the vertical roots which are less branched or unbranched. In some roots from the edge of the river, which presumably had been dry for a longer period, the conjugating parenchyma is much less developed.

Some seedlings were also examined; these did not show any trace of the peculiar roots, but since the seeds germinate and start life on the dry banks and not in the river-bed, this is not so remarkable. In general structure the roots of these seedlings are very like those described, but without the great cortical lacunar system.

The roots of *Terminalia* differ markedly from the pneumatophores of *Sonneratia*,[1] in not possessing the striking peripheral layer of cork with lenticels characteristic of the latter genus. Even old roots of *Terminalia* which had cast off the primary cortex had no lenticels. The hypodermal layer of cells in *Terminalia* is not connected with a cambial layer, and no openings communicating with the outside air occur in it. Another point in which roots of *Terminalia Arjuna* differ from typical pneumatophores is the complete absence of stem characters, such as pith, etc.; as far as vascular anatomy goes they are perfectly normal roots. Though these roots seem to be for purposes of aeration, they cannot be described as as true pneumatophores, in Westermaier's sense.[2]

Mr. Burkill suggested from observations made while collecting the material that the aerating roots of *Terminalia* are probably

[1] Goebel. Ber. Deut. Bot. Ges., 1886.

[2] Westermaier. Loc. cit., 1900.

ephemeral, and functional during the wet season only. He considers it as probable that they die off when the rivers run dry. This suggestion appears quite plausible, since, when the soil is dry, the perennial horizontal roots would be in a medium where ordinary respiration is possible. This is a point that can only be settled by further observations of the plants in their native habitat.

SUMMARY.

The vertical roots are for purposes of aeration as shown by the great development of the lacunar system.

The lacunæ in the primary cortex are developed mainly from conjugating parenchyma.

A secondary aerating cortex is produced in old roots in the region of the secondary phloem.

No root-hairs are present, but a root-cap of a peculiar nature is formed.

No direct connexion with the outside air was noted.

These roots have none of the stem characters of typical Mangrove pneumatophores.

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THE INTER-RELATIONSHIPS OF THE BRYOPHYTA,

By F. Cavers, D.Sc.

[Figs. 18–29.]

Marchantiaceæ.

THIS order (the "Marchantiaceæ-Marchantioideæ" of Schiffner) is distinguished from all the lower groups of the Marchantiales by having stalked carpocephala. The thallus has (except in *Dumortiera*) well-developed air chambers, which are either arranged in a single layer or are divided up by partitions so as to form several superposed series as seen in transverse section. When in a single layer the chambers contain assimilating filaments (except in the Astroporæ). The pores on the thallus are either simple and surrounded by a single ring of cells or by several concentric rings, or are barrel-shaped. There are usually well-developed air chambers on the male and female receptacles, and these usually have the barrel type of pore. The antheridia are generally collected into a sharply defined cushion-like receptacle, which in the highest forms represents a branch-system, having several growing-points, and is then (except in *Fegatella*) stalked. The sporogonium is separable into foot, seta, and capsule; well-developed elaters are always present; the capsule opens by the separation of a more or less definite lid, or by splitting into several valves, or by both processes.

The organisation of the carpocephalum, or archegoniophore, varies a good deal in the different members of the order. In the highest forms (Leitgeb's "Compositæ") there are two or more groups of archegonia, developed in centrifugal succession by as many radially arranged branches or growing apices. Owing to the more rapid growth of the upper tissue of the convex receptacle, the archegonia are carried on to the lower surface, and the youngest archegonia then stand nearest the stalk. The succession of the archegonia is, of course, acropetal with reference to each of the archegonium-producing growing-points and centrifugal with reference to the dorsal side of the receptacle itself—not centripetal, as is often erroneously stated. In the disk-like male receptacle of *Marchantia* and *Preissia*, the antheridia do not undergo this inversion, and the radiating centrifugal arrangement of these organs is at once evident.

In his "Compositæ," Leitgeb placed the genera *Lunularia*, *Dumortiera*, *Preissia*, *Marchantia*, and (doubtfully) *Fegatella*. The remaining genera of Marchantiales with stalked carpocephala which were known to him were divided into two groups which he named "Astroporæ" (*Clevea*, *Sauteria*, *Peltolepis*) and "Operculatæ" (*Plagiochasma*, *Reboulia*, *Grimaldia*, *Neesiella*, *Fimbriaria*). In these two groups, and also in *Fegatella*, the female receptacle was believed by Leitgeb to be in all cases merely a dorsal outgrowth of the thallus, the archegonia being developed singly on the periphery of the receptacle and each archegonium becoming enveloped by its own involucre; except in *Clevea* and *Plagiochasma*, however, the stalk of the receptacle has either a single furrow or two furrows, and this was taken by Leitgeb to indicate that the apex of the thallus entered into the formation of the stalk but not into that of the archegonium-producing region itself. The carpocephalum was therefore regarded as representing a single branch, the apex being used up in its development, whilst the "Composite" carpocephalum was interpreted as being composed of a branch system. Although the distinctions upon which Leitgeb founded this classification of the Marchantiaceæ can no longer be maintained, it will be convenient in this résumé to deal with the genera in three groups, corresponding with Leitgeb's "Astroporæ," "Operculatæ," and "Compositæ."

I.—Astroporæ.

Leitgeb named this group from the fact that the radial walls of the cells (arranged in a single ring) surrounding the thallus air-pores are as a rule strongly thickened, giving the pore a star-like appearance in surface view. Apart from the presence of exactly similar pores in other families (*e.g.*, in *Tessellina* and some species of *Plagiochasma*), there are several species of *Clevea* in which this thickening does not occur. However, there is no doubt that the three genera—to which a fourth (*Gollaniella*) has recently been added by Stephani (62) for a Himalayan plant allied to *Clevea*—form a natural group. Their geographical distribution, which presents some very interesting features, has been described by Solms-Laubach (59). The writer found representative species of all three genera (*Clevea hyalina*, *Sauteria alpina, Peltolepis grandis*) growing, often intermingled, in several localities in the Bernese Oberland, and some additional details were made out in the structure and development of the sexual receptacles and of the sporogonia.

In this group the ventral scales are arranged in several series, as in *Corsinia.* The scales do not show the sharply marked apical appendages which are characteristic of the Operculatæ and Compositæ; in this respect the Astroporæ recall the Corsiniaceæ and Ricciaceæ. The air-chambers, which contain no assimilating filaments, are typically arranged in a single series, but in the median portion of the thallus they are divided up by secondary partitions. The capsule wall has well-developed fibrous thickenings in its cells; there is a small apical cap, and the capsule opens by irregular teeth.

In *Sauteria* and most species of *Clevea* the antheridial group is not sharply separated from the surrounding tissue, the antheridia being developed in long patches arranged in two irregular rows on the midrib; between the antheridial chambers, which have long ostioles, there are air-chambers, and the whole arrangement is hardly more definite than in various species of *Riccia.* In *Clevea Rousseliana* we get the first step towards the differentiation of a definite male receptacle, the group being shorter and the antheridial chambers more closely approximated to each other. In *Peltolepis* the antheridia are developed in definite rounded cushion-like receptacles, sharply marked off from the thallus and surrounded by a series of scales.

The chief interest of the group, however, lies in the organisation of the female receptacle (Fig. 18). In *Clevea* the receptacle arises as a dorsal outgrowth of the thallus tissue immediately behind the growing-point, which, after the young receptacle has been laid down, produces ordinary thallus tissue; and several receptacles may be formed in succession on the same branch of the thallus. The first archegonium is formed at the hinder end of the receptacle, and is followed by one at either side and finally one at the front. In the meantime the lower tissue of the receptacle has become a short stalk, which later lengthens out and carries up the receptacle with the sporogonia; while the archegonia, which at first stand vertically at the edge of the receptacle, are carried downwards owing to growth of the tissue above them, and at the same time each archegonium becomes enveloped by a sheath which grows out from the surrounding tissue. The curved necks of the archegonia at first project freely from the sheath (involucre) and are directed upwards. Scales grow out from the tissue below the archegonia, and when the stalk lengthens these scales are carried up with the receptacle. The whole structure is apparently a mere dorsal outgrowth of the thallus tissue, the apical growth of the thallus not being arrested by the development of a receptacle. The receptacle of *Clevea* may therefore be compared with the outgrowth which arises among the archegonia in *Corsinia*, but in *Clevea* the archegonia do not appear until the outgrowth has developed into a nearly hemispherical structure, about 0·1 mm. in diameter, and when they do appear they arise from the tissue of the outgrowth itself.

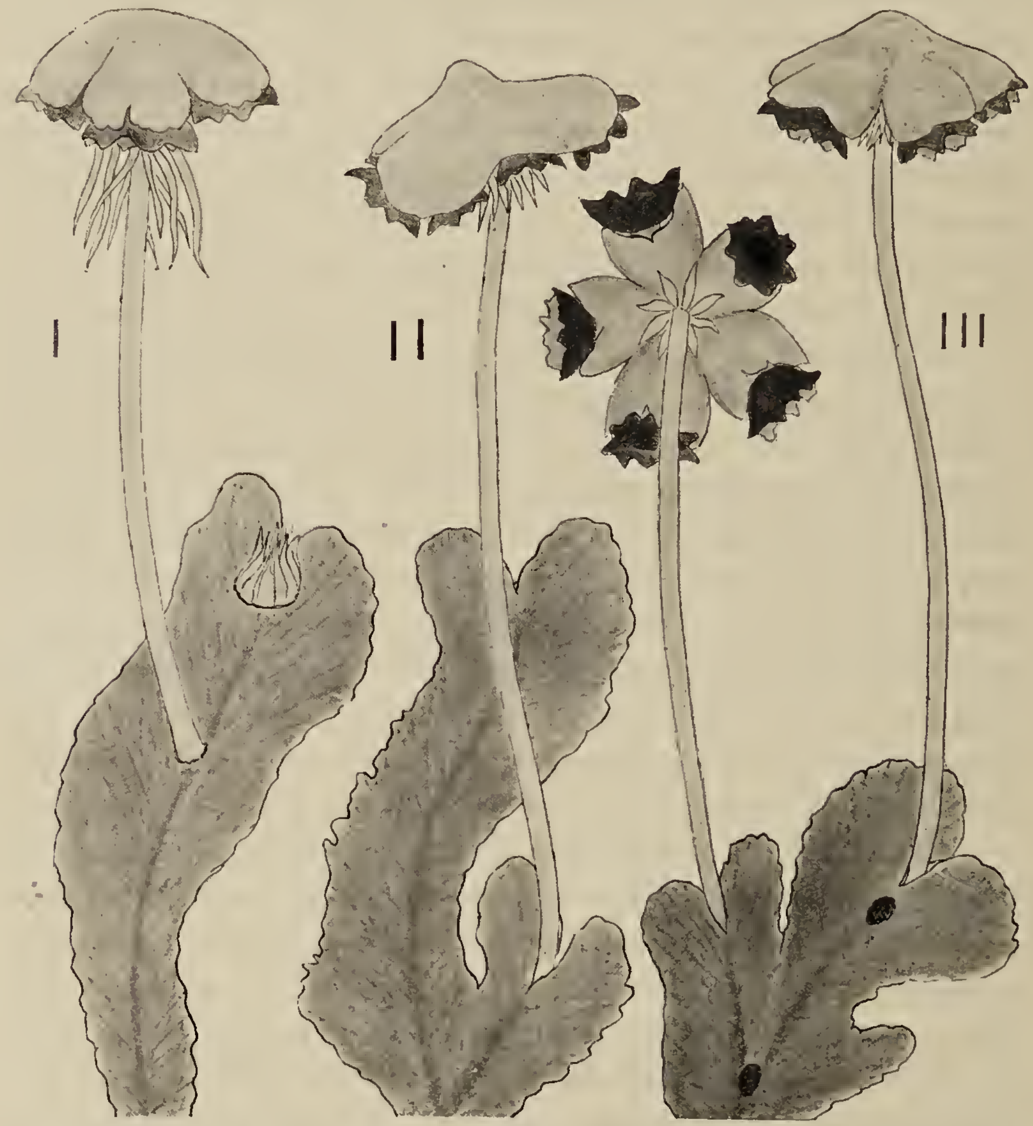

Fig. 18. *Astroporæ.*—I, *Clevea hyalina*; II, *Sauteria alpina*; III, *Peltolepis grandis.*

In *Sauteria* the receptacle begins in the same way as in *Clevea*, but the apical growth of the thallus is arrested when a receptacle is formed, hence a branch of the thallus bears a single receptacle only. According to Leitgeb, a single archegonium is present in each involucre and a single groove in the stalk. The writer found, however, several specimens of *S. alpina* with involucres each containing from two to four archegonia; in some cases two sporogonia had developed in an involucre, and frequently the stalk had two furrows containing the rhizoids, which spring from the underside of the receptacle between the involucres.

Apart from the constant occurrence of two rhizoid-furrows in the stalk, *Peltolepis* agrees closely with *Sauteria* in the structure of the carpocephalum. In *P. grandis*, which Leitgeb and other writers describe as resembling *Clevea* and *Sauteria* in having a single archegonium in each involucre, numerous cases were observed in the writer's Swiss specimens, in which each involucre had two, three, four, and even five archegonia in an involucre, though only one sporogonium was produced in the plants examined. Hence in both *Sauteria* and *Peltolepis* the carpocephalum is of the "Composite" type.

The Astroporæ form an interesting series, marked off from the other Marchantiaceæ by the structure of the thallus and by the scattered and simple ventral scales; while they are still more sharply distinguished from the Operculatæ by the structure of the capsule-wall.

II.—Operculatæ.

Leitgeb named this group from the mode of dehiscence of the capsule in the genera known to him. The capsule-wall has an apical lid which is either thrown off entire or breaks up irregularly, and the lower part of the dehisced capsule remains as an urn, usually with toothed margin. The cells forming the capsule-wall are devoid of special fibrous thickenings, though in the upper half of the capsule the cells often have their radial walls slightly thickened at the corners. From the Astroporæ the group is further distinguished by several other characters: the ventral scales are in two rows and have well-defined apical appendages (sometimes two or three to each scale); the pores on the thallus are surrounded by several concentric rings of cells; the pores on the sexual receptacles are barrel-shaped. It is more difficult to separate the Operculatæ from the Compositæ, for in all the genera, except *Plagiochasma* and and the incompletely known new genus *Massalongoa*, more than one archegonium may be developed in each involucre of the carpocephalum, and among the Compositæ there are genera which resemble the Operculatæ in thallus structure (*Bucegia*) and in the absence of fibres from the capsule-wall (*Lunularia*). Still, the group may be regarded as forming an independent series, showing some striking parallelisms with the Astroporæ on one hand and the Compositæ on the other. In the structure of the carpocephalum

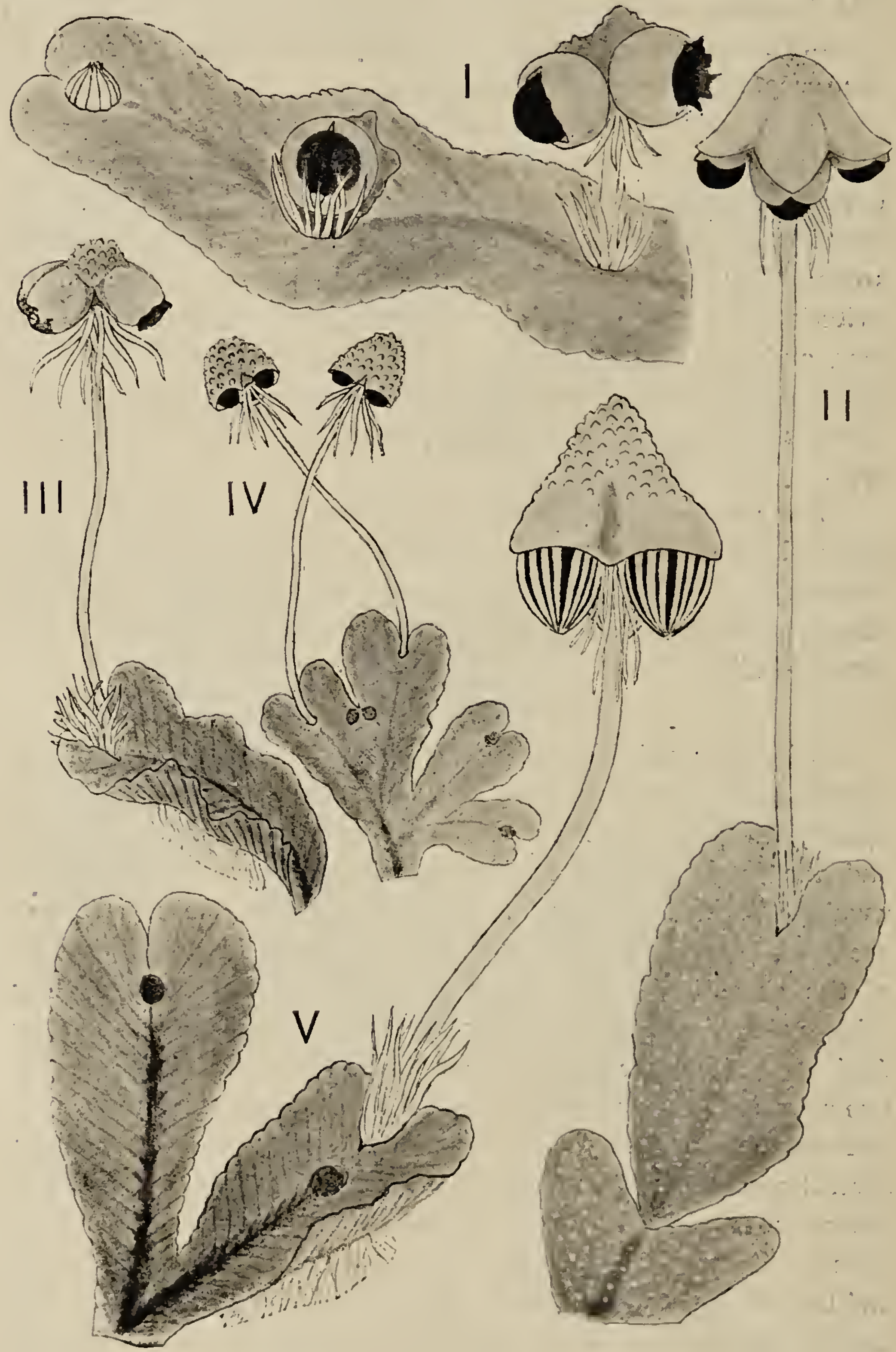

Fig. 19. *Operculatæ.*—I, *Plagiochasma rupestris*, female plant with three carpocephala; II, *Reboulia hemispherica*, with a carpocephalum; III, *Grimaldia fragrans*; IV, *Neesiella rupestris*, with two carpocephala and four male receptacles; V, *Fimbriaria Lindenbergiana*, with a carpocephalum and two male receptacles.

the genus *Plagiochasma* corresponds to *Clevea*, *Reboulia* to *Sauteria*, while the highest forms show a distinct approach to the Compositæ.

The air-chambers of the thallus are usually divided up by secondary partitions and plates, so that the whole upper region appears in section as a spongy mass of green tissue (Fig. 20). In some cases, however, the chambers are in a single layer and are then either empty (*Grimaldia pilosa*, *Neesiella*) or contain assimilating filaments (some species of *Grimaldia* and of *Fimbriaria*).

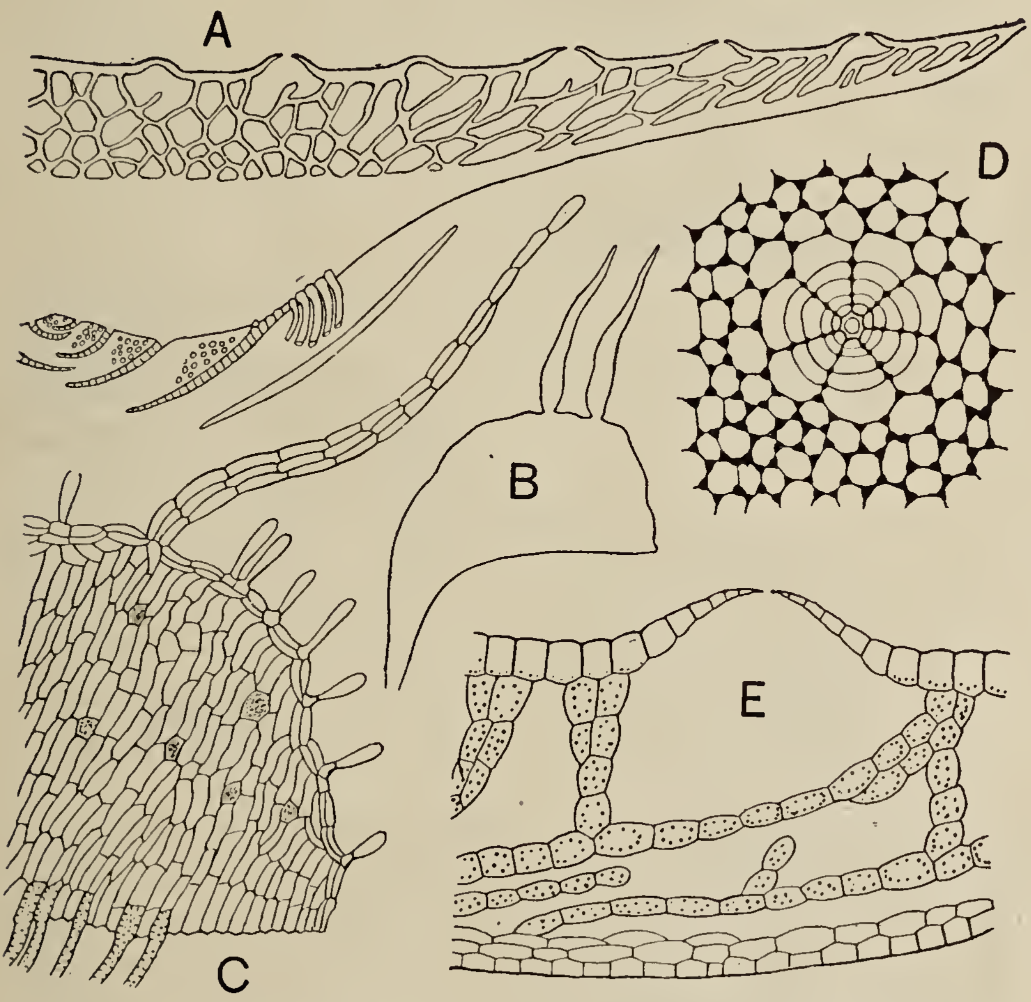

Fig. 20. *Reboulia hemispherica.* A.—Part of a transverse section of the thallus, showing the dorsal zone of green air-chamber tissue and the ventral zone of compact colourless tissue. On the midrib are shown the ventral scales in section, the small tuberculate rhizoids, and the large smooth-walled rhizoids. × 35. B.—A ventral scale, showing two long narrow appendages. × 35. C.—Part of a scale, showing one of the appendages, several marginal mucilage-hairs, some of the oil-cells (shaded), and some tuberculate rhizoids springing from the base of the scale. × 150. D.—Part of the dorsal epidermis in surface view from above, showing a pore surrounded by six concentric rings of cells, the walls of which, as in the rest of the epidermis, show angular thickenings. × 150. E.—Part of A., showing the structure of the lateral region (lamina) of the thallus; the compact ventral tissue is here reduced to two or three layers of cells. × 150.

The male receptacles are marked off from the surrounding tissue by a groove, from which arise scales that cover the receptacle when young. The receptacle is rounded or oval, with a single anterior growing-point which produces the antheridia in acropetal succession; sometimes the apex branches during the development of the antheridia, so that the receptacle is forked in front (Fig. 21, c).

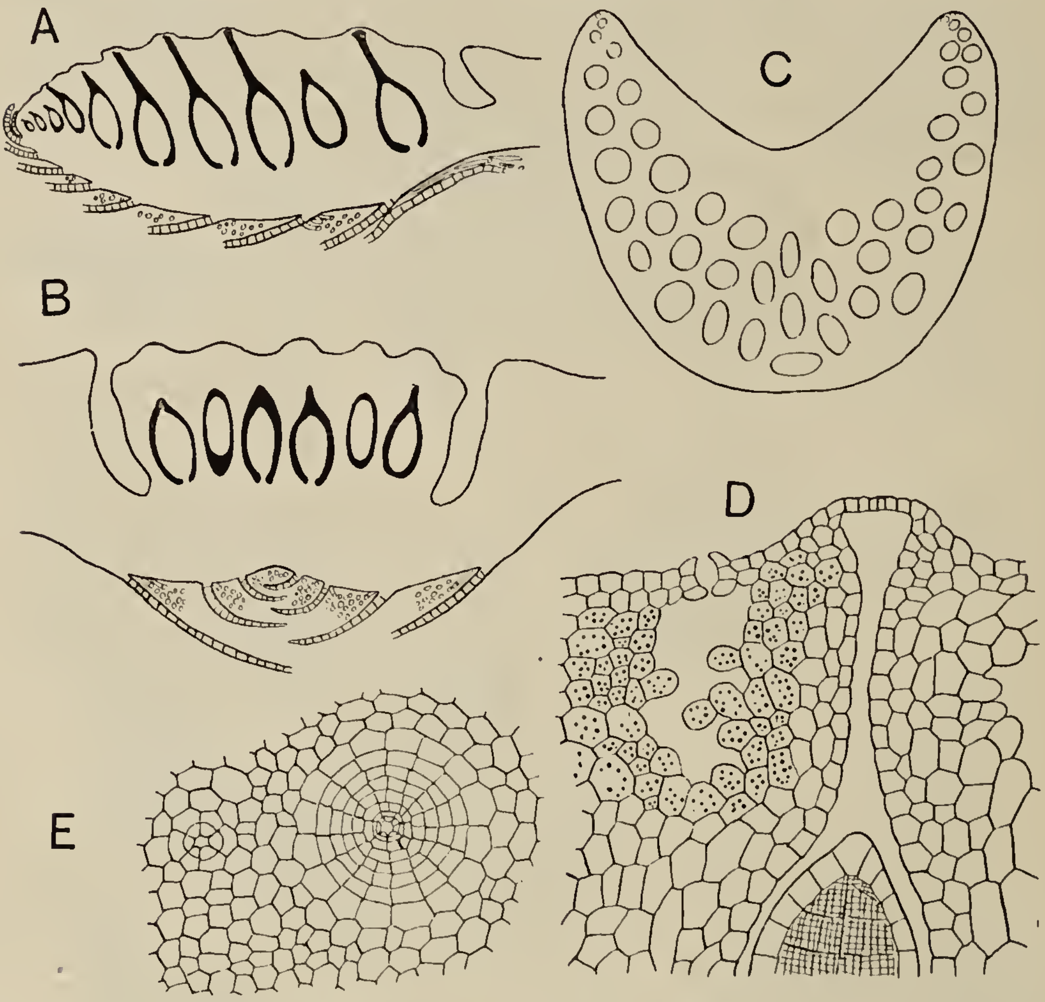

Fig. 21. *Reboulia hemispherica.* A.—Longitudinal section of male receptacle the antheridial cavities are shaded, and the scales and rhizoids on the ventral surface are shown in part. × 20. B.—Transverse section of male receptacle. × 20. C.—Horizontal section of a receptacle with two growing-points, the latter showing the youngest antheridia, whilst the oldest occupy the posterior part of the receptacle. × 20. D.—Part of A, × 150, showing on the right the upper portion of an antheridium and its cavity, on the left an air-chamber opening by a small barrel shaped pore; the cells around the air-chamber contain chloroplasts.

The growing-point may proceed to form ordinary tissue again, leaving the receptacle behind, and several receptacles may be produced one after another; or a female receptacle may be formed immediately in front of the male receptacle; or the apical growth may cease after the development of a male receptacle so that the latter stands at the margin of the thallus.

Plagiochasma (Fig. 19, I.), which stands at the base of this group, strikingly resembles *Clevea* (and differs from all the remaining Operculates) in the development of the carpocephala. The latter are purely dorsal outgrowths, formed one after another; the stalk has no furrow; the central dorsal tissue of the receptacle is poorly developed; hence the bulk of the receptacle is made up of the involucres, each with a single archegonium. In addition to this detailed agreement in the carpocephalum, *Plagiochasma* further resembles *Clevea* in having usually a single ring of cells around each pore on the thallus, and in these cells radial thickening characteristic of the Astroporæ. Four archegonia are usually formed, but frequently only two or three sporogonia, or even a single sporogonium may come to maturity. The upper portion of the capsule-wall

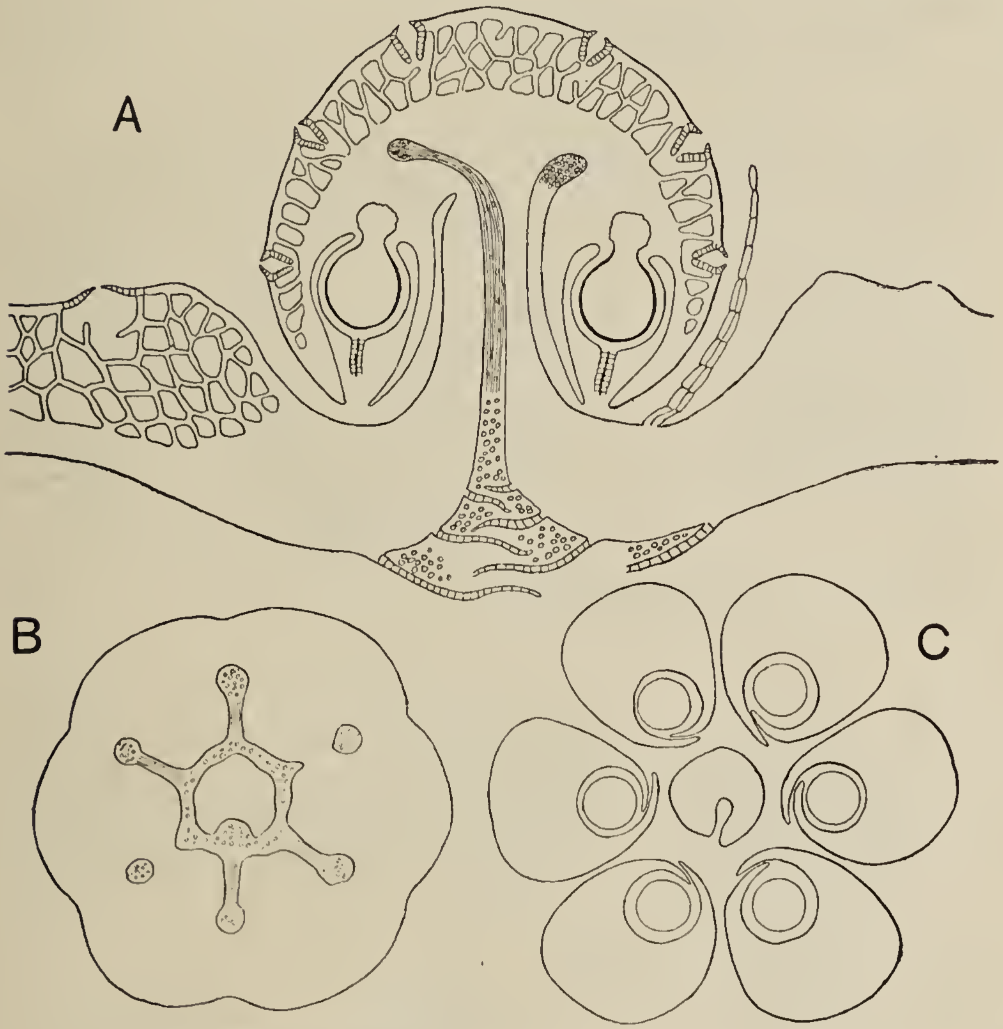

Fig. 22. *Reboulia hemispherica.* A.—Vertical transverse section of a female receptacle and the adjacent portions of the thallus. Two developing sporogonia are shown, each enclosed in its calyptra. The outer portion of the receptacle shows air-chambers with barrel-shaped pores, the inner portion consists of compact starch-bearing tissue, and the groove of the receptacle stalk shows in its upper portion numerous tuberculate rhizoids, in its lower portion a number of ventral scales. On the right, one of the band-like scales is shown arising from the tissue at the base of the stalk. ×20. B and C.—Two horizontal sections of a female receptacle. ×20. A is from the upper portion of the receptacle and shows the six cavities from which spring tuberculate rhizoids, the latter passing into the groove on the ventral surface of the stalk. B is taken at a lower level and shows six sporogonia in outline, each in its involucre.

consists of two to four layers of cells, forming a cap which breaks into fragments when dehiscence occurs. The young carpocephalum is protected by two rings of scales; when the stalk elongates the inner scales are carried up on the receptacle, while the outer scales remain at the base of the stalk.

In all the other genera of Operculatæ, the carpocephalum stalk has a rhizoid groove, and the development of a carpocephalum terminates the growth of the thallus.

In *Reboulia* (Figs. 19-23), which is the only genus represented in

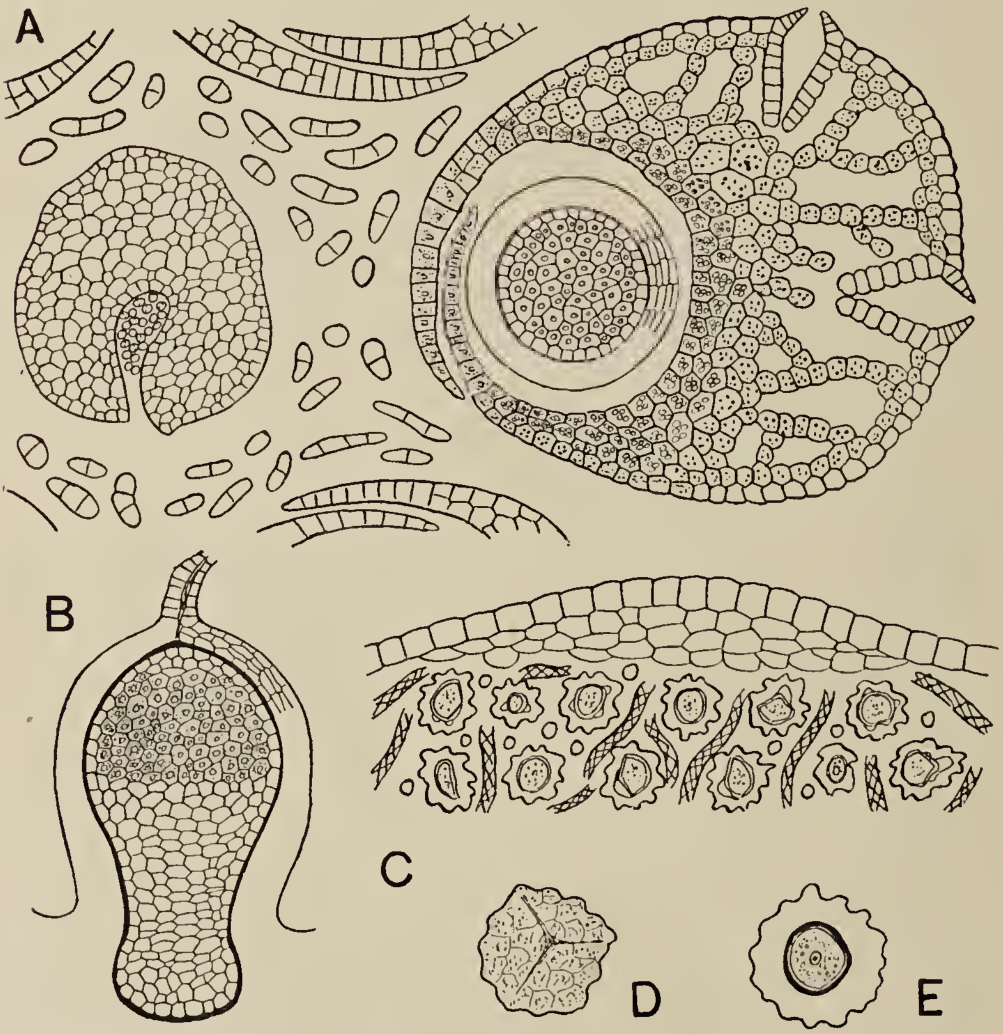

Fig. 23. *Reboulia hemispherica.* A.—Part of Fig. 6, C., × 90, showing on the left the receptacle stalk with it ventral rhizoid-bearing groove, on the right one of the lobes (involucres) with a sporogonium enclosed in the calyptra. The outer portion of the lobe shows air-chambers, opening by large barrel-shaped pores, the inner portion consists of compact starch-bearing tissue. Between the stalk and the involucre are shown the narrow scales in cross-section. B.—Longitudinal section of a young sporogonium, with its calyptra. In the upper portion (capsule) of the sporogonium the archesporial tissue is shaded. × 90. C.—Upper portion of a nearly ripe capsule in longitudinal section, showing the lens-shaped apical cap and some of the spores and elaters. × 120. D.—Spore in surface view, from the inner side, showing the three radiating ridges. The surface is covered with a network of smaller ridges. × 200. E.—Spore in section, showing the thin endospore, the exospore (shaded), and the thick outer coat (epispore) with its ridges. × 200.

Britain, the carpocephalum, which has well-developed air-chambers, is conical or hemispherical when young, with four to seven thick lobes, the margins of which form bivalved involucres, each with a single archegonium (sometimes two archegonia). When the capsules ripen, the lobes spread upwards and outwards, so that the receptacle becomes nearly horizontal. The apical portion of the capsule-wall, which has a well-developed cap (Fig. 23), falls away in fragments when the capsule opens. The series of figures given here will serve to illustrate the structure of this plant, which forms a good average type of the Operculatæ.

Grimaldia (Fig. 19, III.) and *Neesiella* (Fig. 19, IV.) are closely allied to *Reboulia*, but the upper portion of the capsule-wall becomes detached in a single piece, forming a well-defined lid. The limit of the latter, and the dehiscence of the capsule, are in these two genera determined by an annulus consisting of small cells, which does not occur in any of the other Operculatæ. Moreover, in these genera the sinuses from which spring the rhizoids that run into the furrow of the carpocephalum stalk bulge slightly outwards and are visible as short lobes on the outer surface of the carpocephalum, alternating with the bell-shaped involucres; these lobes correspond with the long hollow rays seen in *Marchantia*. In both genera, also, the writer has found that the involucres frequently contain two (*Grimaldia fragans*, *G. dichotoma*) or as many as four (*Neesiella rupestris*) archegonia. The archegonia have usually been described as occurring singly in the involucres, though Leitgeb noted the occurrence of two archegonia in one case in *Neesiella*. In one specimen of *Grimaldia fragans* the writer found two sporogonia in an involucre, but in several cases every involucre examined had two archegonia.

In *Cryptomitrium*, Abrams (1) has shown that each involucre contains a group of archegonia (usually five) which show centrifugal development exactly as in the Compositæ. Moreover, Stephani (61) states that the stalk often has two furrows, and we have here again a typical "Composite" carpocephalum, with five or six growing-points from which the archegonia are developed.

The large genus *Fimbriaria* differs from the other Operculatæ in having a special envelope (perianth) around each archegonium, arising from the tissue inside the involucre; in this respect the genus resembles the highest types of the Marchantiaceæ (*Preissia* and *Marchantia*). The recently discovered Himalayan genus *Massalongoa* is said by Stephani (62) to stand near *Fimbriaria*, but it has no perianth. The perianth of *Fimbriaria* is a striking and beautiful structure (Fig. 19, V.), giving the fruiting carpocephalum a very characteristic appearance, since it protrudes beyond the involucre and its margin is cut up into from four to sixteen long narrow segments, which in some species remain attached at the tips and serve to bring about the gradual dispersal of the spores by acting as a "censer mechanism." Campbell (8) has shown that in *F. californica* the carpocephalum is "Composite," as in *Cryptomitrium*, each of the four involucres containing a group of four archegonia as a rule. In *F. Lindenbergiana*, several receptacles were found by the writer to contain two, three, or four archegonia in some of the involucres, and probably the same will be found in other species of this genus.

III.—Compositæ.

This group contains eight genera—*Exormotheca*, *Fegatella*, *Lunularia*, *Wiesnerella*, *Dumortiera*, *Bucegia*, *Preissia*, and *Marchantia*, all poor in species except *Marchantia*.

The air-chambers are arranged in a single layer, except in *Bucegia* where they are partitioned up as in *Reboulia* and the other typical Operculatæ. There are usually assimilating filaments filling up the chambers, but exceptions occur (apart from *Bucegia*) in the genus *Dumortiera*, in which the air-chamber layer shows great reduction. The extent of the reduction varies in different species, and in the same species according to the conditions of the habitat with reference to moisture and shade. In *D. hirsuta* (in which *D. irrigua* is merged by Stephani) the air-chambers are laid down at the growing-point and, as shown by Coker (17), in plants grown under fairly dry conditions may persist and be roofed over, but in conditions of shade and moisture (in which the plant usually grows) the chambers become disorganised and are only recognisable in the parts behind the apex by the remains of the vertical partitions. In *D. velutina*, the partition-walls and the roofing layer soon become completely disorganised, but the thallus is densely clad with outgrowths corresponding to the assimilating filaments which fill the chambers in other genera. In *D. trichocephala*, according to Campbell (8), there is no trace whatever of the chambers even at the growing-point, but Ernst (20) and Kamerling (29) found that the assimilating filaments are represented by short projecting papillæ. In *Bucegia*, *Preissia*, and *Marchantia*, the thallus pores are barrel-shaped, but in the other genera (as in the Operculatæ) this type of pore is confined to the sexual receptacles, the pores on the thallus being surrounded by concentric rings of cells. In *Exormotheca* the roof of each chamber grows up to form a long chimney-like projection with the pore on its summit; this is merely an exaggeration of the convex form of roof seen in *Fegatella* (Figs. 24, 25).

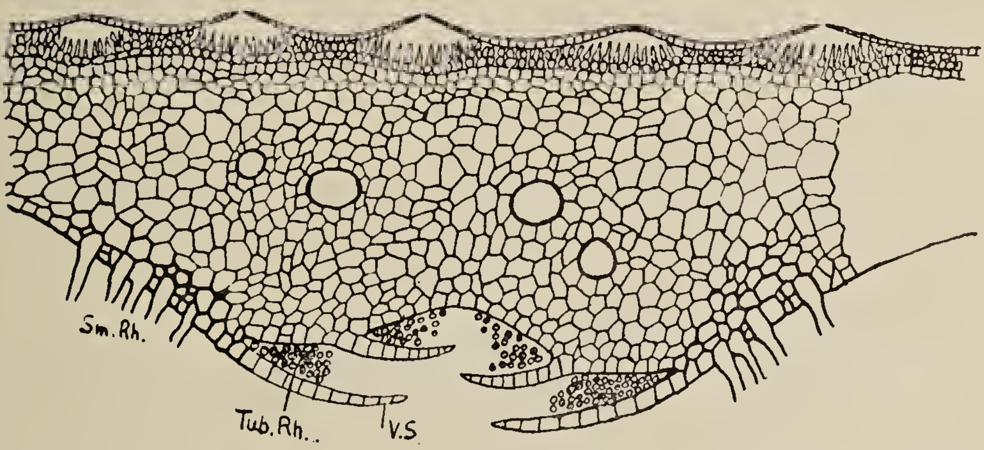

Fig. 24. *Fegatella conica.* Transverse section through midrib of thallus showing the upper zone of air-chambers and the lower zone of compact tissue, with four of the mucilage sacs. Sm. rh., smooth-walled rhizoids; tub. rh., tuberculate rhizoids; v.s., ventral scales. × 30.

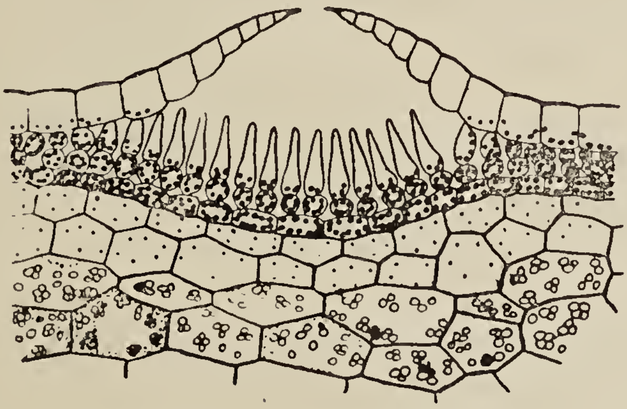

Fig. 25. *Fegatella conica.* Part of a vertical section of the thallus, showing an air-chamber, lined by pointed cells and opening above by a pore in the epidermis. × 180.

In this group the Marchantiaceous thallus reaches its greatest complexity. The compact tissue underlying the air-chamber layer contains large oil-bodies, filling up certain cells; mucilage-sacs, either isolated, or arranged in groups (*Exormotheca*), or in longitudinal rows (*Fegatella*); sclerotic fibres (*Preissia*—Fig. 27—and some species of *Marchantia*); and a mycorhiza (*Preissia, Fegatella*). The ventral scales are generally well developed (except in *Dumortiera*, where they are rudimentary, as might be expected from the hygrophilous habitat), and have an apical appendage separated from the rest of the scale by a deep constriction; the appendages of the younger scales curl upwards over the growing-point (Fig. 26).

The male receptacles are sessile in the lower genera. The simplest type is seen in *Exormotheca*, where the antheridial chambers are developed in a zigzag row along the middle of the thallus. In *Lunularia* the receptacle has the same structure as in *Reboulia*; the antheridia, which are developed in acropetal succession, are peculiar among Marchantiales in having a long slender stalk. In *Wiesnerella*, *Fegatella*, and *Dumortiera*, the receptacle evidently represents a branch-system, since the antheridia are (especially in *Fegatella*) clearly arranged in several radiating rows. In *Bucegia*, *Preissia*, and *Marchantia*, the receptacles are definitely radial and lobed (palmate in some species of *Marchantia*), with a zigzag row of acropetally developed antheridia to each lobe, and the receptacle is raised above the thallus on a stalk with two furrows; here the receptacle is undoubtedly a branch-system, having as many growing-points as there are lobes.

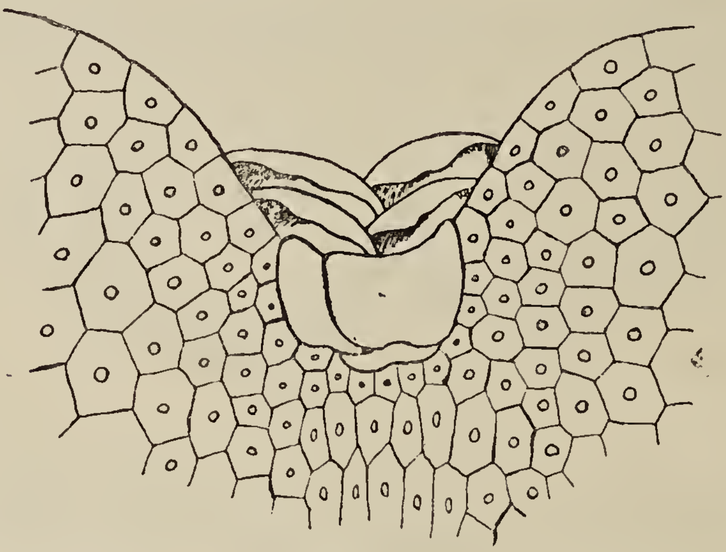

Fig. 26. *Fegatella conica*. Growing point from above, showing the reflexed scales and the areolation of the thallus. × 10.

The carpocephala vary considerably in structure, but in all cases they are terminal on the thallus and each involucre contains a group of archegonia, except in *Fegatella* where there is but one archegonium as a rule. The simplest carpocephalum is that of *Exormotheca*, which has two involucres, standing right and left; the central tissue above and between the involucres is little developed, as in *Clevea* and *Plagiochasma*, but the stalk has a furrow and the involucres contain several archegonia. *Lunularia* is exceptional in that the carpocephalum stalk has no furrow, but in the remaining genera there are two furrows. In *Wiesnerella*, with six to eight involucres, and in *Dumortiera*, with as many as sixteen, the receptacle is like that of *Fegatella* in external appearance; but in *Preissia* and *Bucegia*, which have four involucres, the rhizoid-

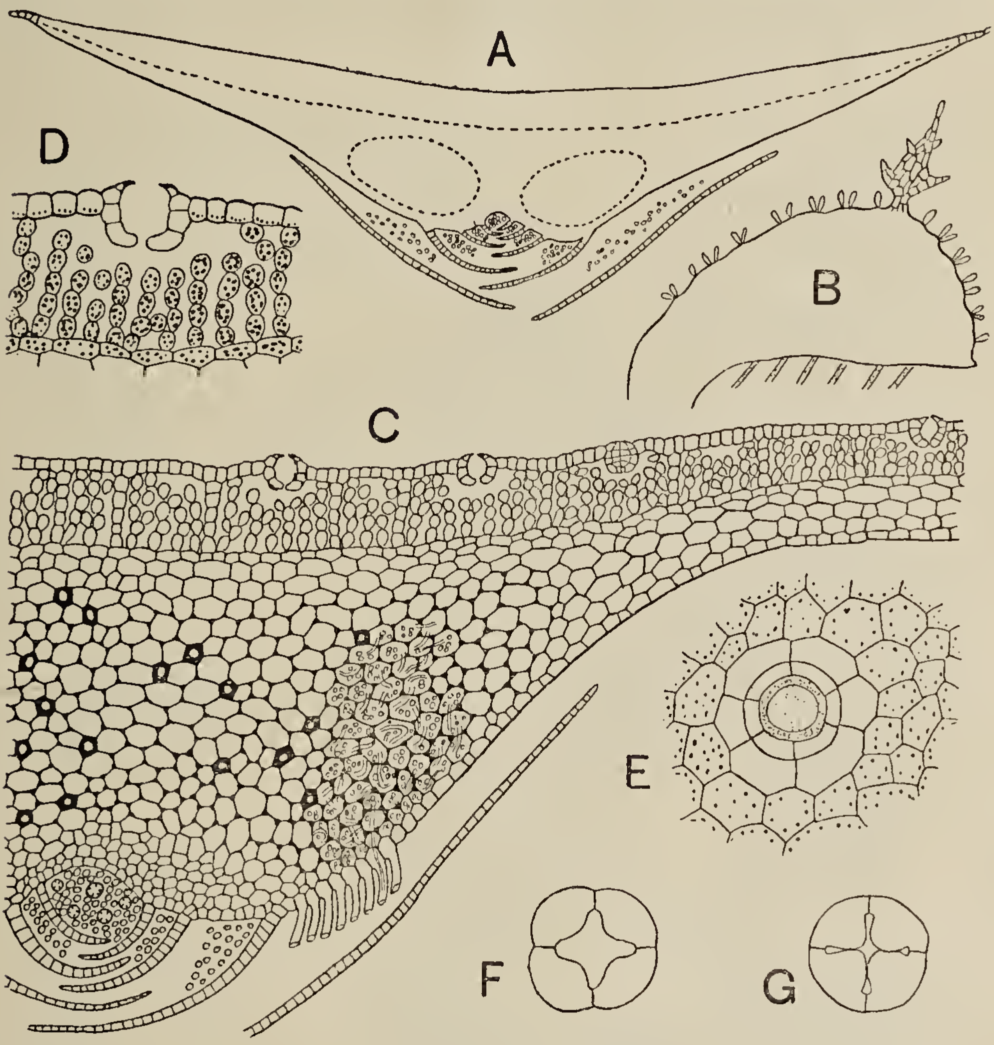

Fig. 27. *Preissia commutata*. A.—Transverse section of thallus. The two areas enclosed by dotted lines indicate the position of the mycorhiza, and the depth of the air-chamber zone is shown by the upper dotted line extending across the thallus. At the margins there is a membrane one cell thick and four or five cells broad. × 20. B.—A ventral scale, showing its pointed appendage, the club-shaped mucilage hairs on the free margin, and some of the tuberculate rhizoids springing from the base of the scale. × 35. C.—Part of A., × 60, showing the upper zone of air-chambers and the lower zone of compact tissue. In the latter, part of the mycorhiza is shown with fungal hyphæ, and one of the latter is seen entering by a smooth-walled rhizoid on the side of the midrib. On the lower side are shown the overlapping scales and the bundles of tuberculate rhizoids. D.—Part of C., × 120, to show the structure of an air-chamber. The floor of the chamber consists of green cells, and from it arise branched green filaments. Chlorophyll is also present in the epidermal cells. E.—Part of the epidermis in surface view, from above, showing two rings of cells around the pore, with the thin membrane covered with resinous grains. The dotted lines indicate the position of the lowest ring of cells. × 200. E and F.—The lowest ring of cells in surface view, from below. In E the pore is open, in F it is almost completely closed. × 200.

bearing sinuses alternating with the involucres project outwards as ridges (Fig. 28, A and B).

The species of *Marchantia* differ a good deal in the organisation of the carpocephalum. The simplest type is seen in *M. geminata*.

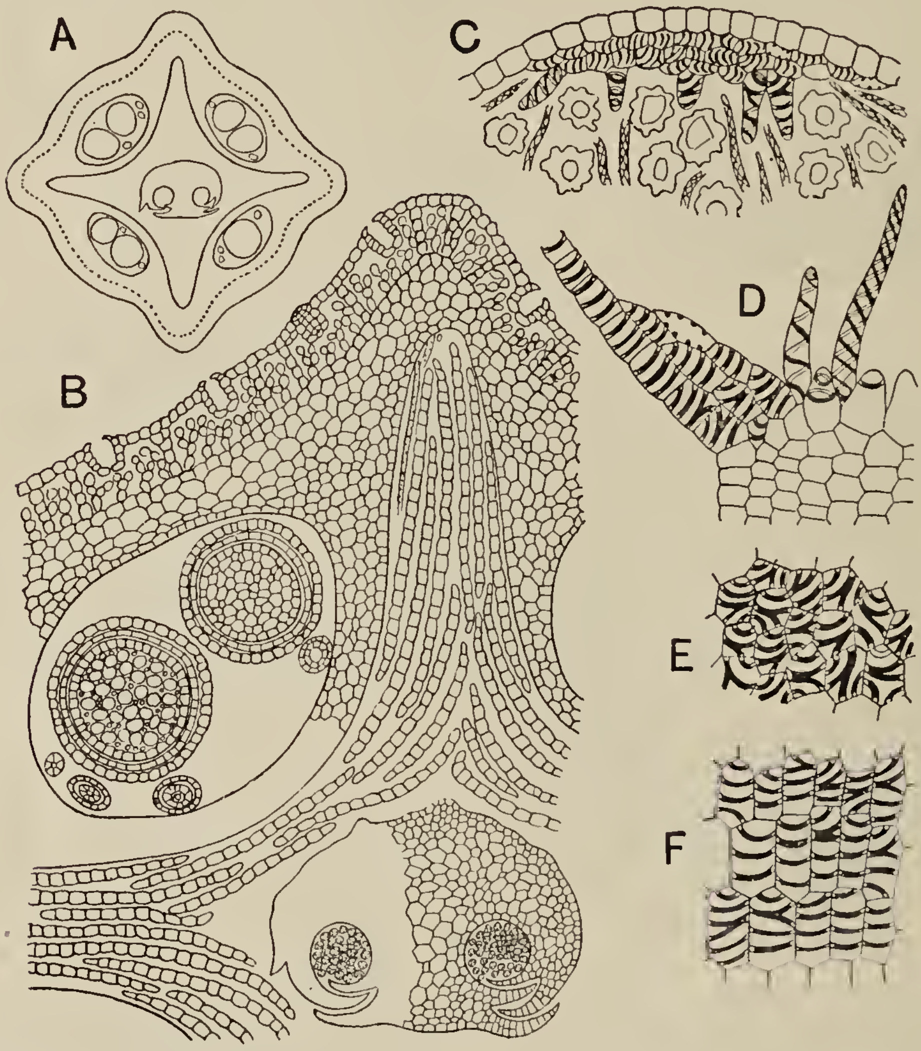

Fig. 28. *Preissia commutata*. A.—Horizontal section of a female receptacle, showing the four lobes and the alternate archegonial groups with young sporogonia and unfertilised archegonia. × 15. B.—Part of A, × 60, showing the receptacle-stalk with its two ventral rhizoid-grooves and one of the archegonial groups in which two sporogonia are developing. Beside the young sporogonia are shown four unfertilised archegonia. The outer tissue of the receptacle contains air-chambers, the inner tissue contains abundant starch-grains, and the hollow lobe is nearly filled with scales, seen in section. C.—Upper portion of a nearly ripe capsule in longitudinal section, showing the lens-shaped apical cap, the cells of which bear ring-like fibres and from which there project some fixed elater-like cells. × 90. D.—Lower portion of capsule in longitudinal section, showing the basal thickening of the capsule-wall and the fixed elaters occupying the bottom of the capsule. × 90. E and F.—Capsule-wall in surface view. E is from the upper, F from the lower portion of the capsule. × 90.

Here the carpocephalum has four spreading flat branches, each of which is notched at the free end and bears on its underside a group of archegonia surrounded by an involucre, the latter being formed by the downward growth of the tissue of the branch and somewhat resembling the bilobed involucre of *Targionia*. In most species of *Marchantia*, however, there are, alternating with the involucres, hollow lobes from which spring the rhizoids that pass into the furrows of the stalk. In *M. polymorpha* these lobes grow out to form long hollow rays, of which there are generally nine—one in excess of the number of involucres. The same numerical relation is seen in other species of *Marchantia* with alternating involucres and lobes; the number of involucres varies from four to ten, and there is always one involucre short as compared with the number of lobes. However, the morphology of the carpocephalum will be discussed presently in considering the phylogeny of the Marchantiales.

The capsule-wall has ring-fibres, except in *Lunularia* where their complete absence recalls the capsule structure of the Operculatæ. In *Fegatella*, *Lunularia*, and *Dumortiera* there is a well-developed apical thickening which is thrown off as a lid, the lower portion of the capsule then splitting into from four to eight teeth. In the other genera the apical cap is only indicated by an imperfect or loose layer of cells lying within the normally single-layered capsule-wall at the apex, and the capsule opens by teeth extending to the apex.

PHYLOGENY OF THE MARCHANTIALES.

From our survey of the Marchantiales, it is evident that on the whole we can trace within this phylum, starting from *Riccia*, a general advance in the elaboration of the vegetative organs, the aggregation of the sexual organs into gametophores of increasingly complex organisation, and a progressive differentiation of the sporogonium.

The simplest thallus structure is that seen in most species of *Riccia*, where the upper tissue consists of filaments separated by narrow air-spaces. But within the genus *Riccia* itself we find the higher type of assimilating tissue which is characteristic of the Marchantiales as a whole—the widening of the spaces to form roofed-over chambers, with or without the partitioning up of the chambers so as to form a spongy mass of tissue. In the higher Marchantiales, practically the only further advances made in the elaboration of the air-chamber zone are the development of assimilating filaments by outgrowth of the cells forming the floor of the uniseriate chambers (*Corsinia*, *Boschia*, *Targionia*, some species of *Grimaldia* and *Fimbriaria*, all the Compositæ except *Bucegia*); and the elaboration of the pores, which may remain surrounded by a single ring of cells with thickened radial walls, or may have several concentric rings of cells, or superposed tiers of cells forming a barrel-like structure. The elaboration of the thallus has clearly taken place independently in several distinct lines, and is only in a very general way correlated with the advance made by the members of each line in other respects.

Much the same may be said of the sporogonium. The early stages in differentiation are, to so speak, hurried through in the lower Marchantiales, and then the sporogonium makes practically no further advance. From the sterilisation of a single peripheral layer (*Riccia*) we pass to that of certain archesporial cells—serving at first for nutrition (*Corsinia*) and then acquiring the additional function of assisting in spore-dispersal by becoming thickened locally (*Boschia* shows the beginnings of this)—and to the differentiation of foot, seta, and capsule. The capsule-wall remains one cell thick, except for the apical cap found in Targioniaceæ and Marchantiaceæ, and (except in Ricciaceæ, *Corsinia*, the Operculatæ, and *Lunularia*) acquires fibrous thickenings. Except in a very general way, the sporogonium affords very little guidance to the phylogeny of the Marchantiales. Taken along with other characters, however, it helps in indicating the probable relationships of the groups.

The sexual receptacles, on the other hand, show a wide range of organisation, starting from *Riccia*, where the individual sexual organs are scattered over the median portion of the thallus, each antheridium and archegonium sunk in its own cavity, and leading to the complex stalked gametophores of *Marchantia*. The evolution of the male receptacle need not be traced in detail, but it may be noted that once the antheridia have been aggregated into receptacles and the latter have by a further step been sharply defined from the ordinary thallus tissue, the further advance of the male receptacle has, so to speak, lagged behind that of the female receptacle. Only in the highest members of the phylum does it become a definite branch-system with several growing-points, raised above the thallus on a grooved stalk. In the forms intermediate between these highly organised types and the Ricciaceæ, the male receptacle is at the most a mere ridge or cushion borne dorsally on the thallus or situated terminally on a branch whose growing-point is used up in the development of the receptacle.

It is not difficult, on biological grounds, to understand why the female receptacle should have made more rapid advance in elaboration than has been the case with the male receptacle. The function of the antheridia is accomplished when they have matured and liberated the antherozoids; but the archegonia and the tissues surrounding them are concerned with the important and often prolonged processes of nourishing and protecting the developing sporogonia. Moreover, the working out of efficient methods for spore-dispersal has clearly played an important part in the evolution of the carpocephalum, and the first decided step in this direction would be the elevation of the sporogonia above the general surface of the thallus.

The starting point in the evolution of the carpocephalum is evidently to be found in the Corsiniaceæ, which are not very far removed from the Ricciaceæ. No known species of *Riccia* shows a definite archegonial group, but in *Tessellina* we get an approach to a female receptacle, for the archegonia are no longer sunk in the general thallus tissue. The envelope which grows up around each archegonium may be compared with the involucre of higher forms, and if the archegonia were developed in small groups and each group were raised above the thallus on a stalk formed by growth of the underlying tissue, we should have a carpocephalum comparable with that of *Clevea* or *Plagiochasma*. In the latter genera, however, the archegonia are not developed until the receptacle has arisen as an outgrowth behind the growing-point of the thallus, and they are developed upon this outgrowth, each archegonium becoming surrounded by an involucre. The gap between *Tessellina* on one hand and *Clevea* and *Plagiochasma* on the other is to a large extent bridged by *Corsinia*, where an outgrowth arises in the midst of the archegonial group in a depression of the thallus, the outgrowth appearing after the archegonia have begun to develop. In *Corsinia*, therefore, we have a primitive carpocephalum which arises at a late stage as compared with the carpocephalum of *Clevea* or *Plagiochasma*; its further development depends upon the fertilisation of the archegonia, and in any case it never becomes more than a scale which is thrust to one side during the development of the sporogonium, the latter being protected from the first by its own thick calyptra rather than by the incipient carpocephalum.

The affinities of the Targioniaceæ and of *Monoclea* have already been discussed, and we have seen that the involucre of these forms may be directly compared with the hood-like scale which arises behind the archegonial group of *Boschia*. *Cyathodium* has clearly arisen by reduction, correlated with adaptation to a moist and shaded habitat, from a *Targionia*-like type, while the anomalous characters of *Monoclea* may also be explained as due to still more complete adaptation to a hygrophilous or almost aquatic mode of life. These three genera occupy a somewhat isolated position in the Marchantiales, and there is much to be said for the view that they represent an independent line derived from a *Boschia*-like type.

It is hardly an exaggeration to say that, beyond the possession of a stalked carpocephalum, the Marchantiaceæ are not distinguished from the four lower families of Marchantiales by a single character of importance. The Astroporæ form a fairly natural group, marked off from the Corsiniaceæ by the stalked carpocephalum and the well-developed elaters, and from the Operculatæ by the fibrous thickenings in the cells forming the capsule-wall. The Operculatæ and Compositæ, however, form much less natural divisions. The apical thickening of the capsule-wall and the dehiscence of the capsule by the throwing off of a lid are characters found in the Targioniaceæ and in practically every genus of Marchantiaceæ, though apparently it is only in the Operculate genera *Grimaldia* and *Neesiella* that the operculum is definitely delimited by an annulus of small cells. The structure of the thallus is remarkably uniform throughout the Operculatæ, and a second common character is the absence of fibres from the capsule wall, but in all the genera that have been investigated, except *Plagiochasma*, we find an approach to the definitely "Composite" type of carpocephalum. On the other hand, *Fegatella*, which we can hardly place elsewhere than in the Compositæ, resembles the typical Operculatæ in having as a rule a single archegonium in each involucre; while *Bucegia* and *Lunularia* show "Operculate" characters in the air-chamber layer and the capsule-wall respectively. It is hardly necessary to emphasize the contention that the organisation of the carpocephalum affords the best clue to the phylogeny of the Marchantiaceæ. For instance, *Marchantia* and *Lunularia* alone among Marchantiales possess gemmæ, and it is hardly likely, even in a group so rich in examples of homoplasy as the Hepaticæ, that precisely the same peculiar type of gemma should be evolved in widely separated types. Yet the two genera differ widely in apparently important characters; *Marchantia* has barrel-like thallus pores, a stalked male receptacle with several growing-points, a perianth around each archegonium, and ring-fibres in the capsule-wall, while *Lunularia* has simple thallus pores, a sessile male receptacle with a single anterior growing-point, no perianth, and no ring-fibres.

The earliest stages in the development of the carpocephalum of the higher Marchantiales were first fully worked out by the writer for *Fegatella* (14); *Preissia* and *Marchantia* give similar results so far as these stages are concerned. When the formation of a carpocephalum is about to begin, the growing-point of the thallus broadens out and undergoes a first dichotomy, a "middle lobe" being formed between the two new growing-points exactly as in ordinary apical branching. Each of these growing-points becomes broadened and undergoes dichotomy. In *Preissia* branching stops at this stage, but in *Marchantia polymorpha* each of the four growing-points divides again, giving eight growing points; in both genera each of the growing-points eventually produced gives rise to a series of archegonia. In the case of *Fegatella* only two of the four growing points divide again, as a rule, and each of the six growing-points usually produces only one archegonium.

There is every reason for the belief that the carpocephala of all Marchantiaceæ, excepting *Clevea* and *Plagiochasma*, will be found to show the "Composite" mode of development just described, and that the organisation of the fully developed carpocephalum will be found to depend upon differences in detail in the later stages of growth. Thus, the presence in the stalk of a single furrow or of two furrows probably depends upon differences in (1) the rapidity with which the early apical divisions succeed each other and (2) the amount of growth which occurs in the tissue at the base of the developing carpocephalum. The fact that repeated dichotomy of the apex has been demonstrated in the development of the carpocephalum of *Fegatella*, despite the fact that the archegonia are usually produced singly in the involucres—that is, one archegonium from each growing-point—certainly suggests that the carpocephala of all the Marchantiaceæ, except *Clevea* and *Plagiochasma*, represent branch-systems, and that they differ only in such details as form, size, number of furrows in the stalk, presence or absence of projecting rhizoid-sinuses, presence or absence of perianths, number of archegonia produced by each growing-point.

Leitgeb distinguished three types of carpocephalum in the Marchantiaceæ: (1) the *Clevea* and *Plagiochasma* type, with furrowless stalk, and one archegonium in each involucre; (2) the Operculate type, including the Astroporæ, the Operculatæ, and *Fegatella*, with a single groove (two in *Peltolepis*) and a single archegonium in each involucre; (3) the Composite type, with a two-furrowed stalk (except *Lunularia*) and several archegonia in each involucre. The first type of carpocephalum was regarded by Leitgeb as a purely dorsal outgrowth of the thallus; the second as representing a single branch, the growing-point of which is used up in the development of the carpocephalum without undergoing dichotomy; and the third as being composed of a branch-system, the growing-point being not only used up but undergoing repeated dichotomy during the formation of the carpocephalum, this dichotomy occurring at an early stage and affecting the whole carpocephalum and not merely the stalk. As we have seen, however, the facts recently discovered have broken down the distinction between Leitgeb's second and third types, and we are probably justified in regarding the carpocephalum which terminates the apical growth of the thallus as being in all cases formed by repeated dichotomy of the apex, resulting in from two to sixteen growing-points, each of which may produce either a single archegonium or a series of archegonia. In *Clevea* and *Plagiochasma* the carpocephalum when fully developed has much the same structure as in the other Marchantiaceæ which have a single archegonium in each involucre, except for the absence of rhizoids from the receptacle and of a groove from the stalk, and it can hardly be doubted that we have even here a difference in degree rather than in kind as compared with the carpocephalum of other genera. That is to say, the difference between the "dorsal outgrowth" carpocephalum of these two genera and the "branch system" carpocephalum of the other Marchantiaceæ depends upon the behaviour of the growing-point in the early stages of development.

Exormotheca presents what is perhaps the simplest type of a definitely "Composite" carpocephalum, which here consists of a branch system with two growing-points. The apex undergoes a single dichotomy, and each of the growing-points produces a series of archegonia, the latter being developed in centrifugal succession, in each series, with reference to the centre of the dorsal side of the receptacle. This Composite receptacle differs from the *Clevea* type chiefly in the hastening of the events that take place in the laying down of the young carpocephalum. The growing-point now enters into the composition of the receptacle from the very first, undergoing dichotomy and becoming used up in the development of the archegonia, so that the formation of a receptacle necessarily terminates the apical growth of the thallus on which it is borne. The presence of ventral scales and of rhizoids, the latter passing into the furrow of the stalk, may obviously be regarded as confirming the interpretation of the Composite receptacle, found in all Marchantiaceæ except *Clevea* and *Plagiochasma*, as a branch system, which shows increasing complexity in the higher forms of the *Marchantia*-series. The development of a single archegonium in each involucre can no longer be taken as an indication that the carpocephalum differs in nature from the Composite type, but at the same time the inter-affinities of the Marchantiaceæ are difficult to disentangle, and it is probable that the presence of a single archegonium in the involucre is (apart from the cases of *Clevea* and *Plagiochasma*) due simply to reduction and is not a primitive character.

As already pointed out, the evolution of the stalked carpocephalum is closely correlated with the facilitation of spore-dispersal, which has also been the chief factor in the evolution of the sporogonium. In the Ricciaceæ the spores can only escape by the decay of the surrounding thallus tissue in which the sporogonium is embedded (*Riccia*), or that of the envelope projecting above the general level of the thallus (*Tessellina*), in addition to the disorganisation of the thin capsule-wall and calyptra. *Tessellina* marks a great advance upon *Riccia*, in that the sporogonium is raised above, instead of being deeply sunk in, the thallus, and the spores no longer have to wait until the decay of the whole thallus sets them free. With this shifting of the sporogonium to the surface we may correlate its differentiation, first seen in *Corsinia*, into foot and capsule, and the sterilisation (already indicated in *Tesellina*) of some of the archesporial tissue of the capsule. The sterile archesporial cells have the primary function of supplying food to the developing sporogenous cells, and in *Corsinia* this is their sole function. In *Boschia*, however, the sterile cells lose their solid contents before the spores have ripened, and then (having acquired annular and spiral fibrous thickenings) serve for the conduction of water and salts to the developing spores, becoming elongated in order to perform this second function more efficiently. Finally, in the higher Marchantiales the elaters become greatly elongated and assume a third function after the dehiscence of the capsule, namely that of assisting hygroscopically in the dispersal of the spores; along with this we get the provision of mechanisms for the dehiscence of the capsule by means of a lid or of valves, or both, often accompanied by the formation of thickening fibres in the cells of the capsule-wall (already indicated in *Boschia*).

In *Riccia* the developing sporogenous cells readily absorb food from the thallus tissue which surrounds them and from which they are separated only by the delicate single-layered capsule-wall and double-layered calyptra. In *Tessellina* the capsule-wall is separated by several layers of tissue (the two inner layers belonging to the calyptra) from the chambered assimilating tissue of the involucre, but the food supply for the developing spores comes mainly from below, and with this fact we may correlate the presence of a few sterile cells among the fertile spore-mother-cells. In *Corsinia* the sporogenous tissue is well raised above the thallus level by the differentiation of a foot, which acts as an absorbing organ, and the nutrition of the spore-mother-cells is further secured by the numerous starch-laden sterile cells mingled with the spore-mother-cells and exceeding them in number. The protection of the developing sporogonium against desiccation—a function performed in *Riccia* by the surrounding thallus tissue—is in *Tessellina* taken over by the involucre and in *Corsinia* by the massive calyptra. This great development of the calyptra, in which *Corsinia* differs from all other Marchantiales, is evidently a biological adaptation to compensate for the inadequate protection afforded by the incipient carpocephalum; in *Boschia* the calyptra is not nearly so thick as in *Corsinia*, but the hood-like involucre covers the fruit more completely, and persists until dehiscence.

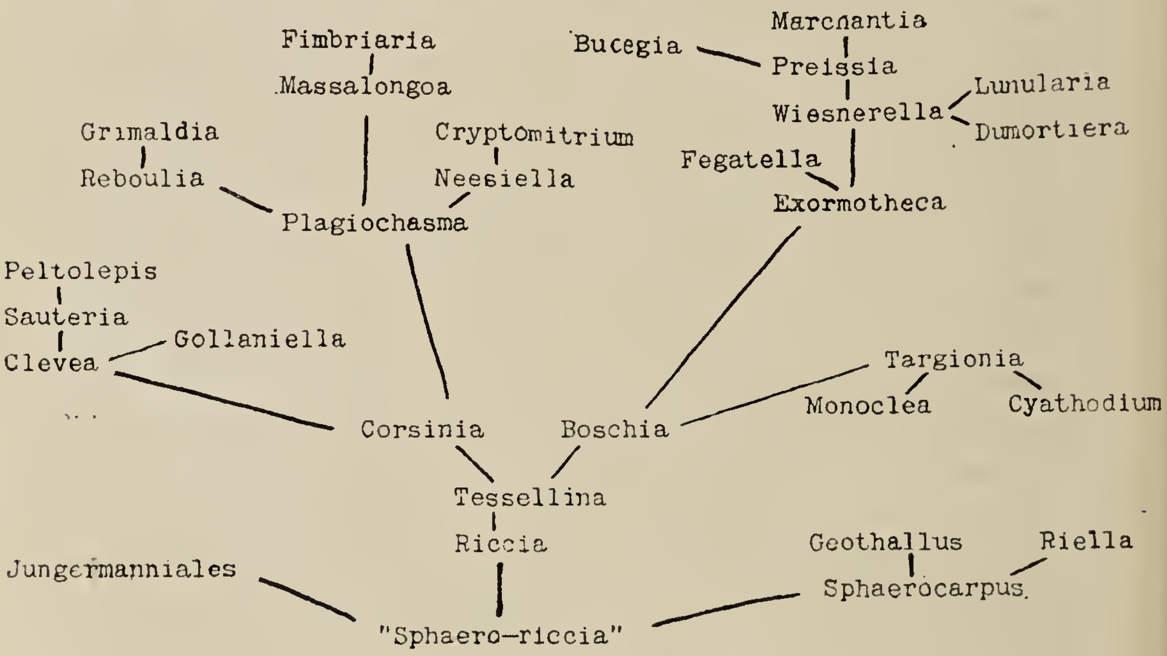

Fig. 29.—Phylogeny of the Marchantiales.

In seeking to trace the phylogeny of the Marchantiales (which, according to the views here advocated, may be roughly represented as in the diagram, Fig. 29), we are confronted by difficulties which involve the phylogeny of the Bryophyta as a whole, and which will be more appropriately discussed later. The study of the geographical distribution of the existing Hepaticæ leads to the conclusion that the thalloid forms at any rate (the Marchantiales and probably also the lower Jungermanniales) are ancient forms. As Campbell (9) has pointed out, the scarcity of fossil Bryophytes may be partly attributed to the delicate and perishable nature of their tissues. At present no conclusions as to the antiquity of the different groups of Bryophyta can possibly be drawn from the very scanty and doubtful Palæozoic remains that have been referred to provisional genera like *Marchantites* and *Muscites*; see Scott's summary (58). The earliest known undoubted fossil Bryophyte is a *Marchantia*-like form (*Marchantites*) found at least as far back as the Jurassic. Judging from the habitats of the existing forms, the only liverworts that might be expected to occur in the Palæozoic rocks are the shade-loving, hygrophilous, and epiphytic species, belonging chiefly to the leafy Jungermanniales. The existing Marchantiales are much more completely adapted to land life, and to life in open and exposed situations, than are the Jungermanniales. Xerophilous forms occur in all the groups of Hepaticæ, but the proportion of such forms is largest in the Marchantiales.

The habitats of the Marchantiales are also of interest in considering the question whether the existing members of this group really form an ascending series starting with Ricciaceæ, or whether the Ricciaceæ, and perhaps also the Corsiniaceæ, are to be regarded, on the other hand, as reduced forms. The only genus of Marchantiales which clearly shows reduction in both gametophyte and sporophyte is *Cyathodium*, and as Lang (35) has pointed out, this genus "is to be regarded as primarily a form adapted to shade conditions rather than as a hygrophyte." In this respect *Cyathodium* forms a contrast to the markedly hygrophilous genera *Dumortiera* and *Monoclea*, in which there is no evident reduction in the sporophyte though the thallus shows extensive or even complete degeneration of the air-chamber layer. In the Ricciaceæ we have a number of hygrophilous species (*Riccia crystallina* and its allies), and in two cases a terrestrial species has a free-floating aquatic form, either swimming (*R. natans*, the aquatic form of *R. lutescens*) or submerged (*R. fluitans*, the aquatic form of *R. canaliculata*), but the only liverwort which fruits under aquatic conditions is *Riella*, and *Riella* is almost certainly derived from a *Sphærocarpus*-like form by adaptation to submerged aquatic life, and cannot be regarded as a primitively aquatic type.

Whether or not the simple structure of the *Riccia* sporophyte is due to reduction, correlated with the sunken position of the spore-fruit in the thallus tissue, remains an open question. On the whole it seems probable that *Riccia* has been derived from a form not unlike *Sphærocarpus* by elaboration of the thallus as an adaptation to life in more exposed and less hygrophilous surroundings, leading in several species to marked xerophily—shown by the large overlapping purple ventral scales and the formation of perennating tubers. But there is a somewhat wide gulf between *Riccia* and the Sphærocarpales, despite the close agreement in the structure and mode of branching of the apical growing-point, the development of the sexual organs, and the embryogeny; for in *Geothallus* and *Riella*, and even in *Sphærocarpus* itself, we find a marked tendency towards the differentiation of a leafy shoot which is characteristic of the Jungermanniales. Campbell suggested that the three great phyla of Hepaticæ (Marchantiales, Jungermanniales, and Anthocerotales) may be derived from a primitive form (Lotsy's "Sphæroriccia") which combined the simple thallus of *Sphærocarpus* with a *Riccia*-like sporophyte. And, as pointed out by Tansley (63), the Protobryophytes probably arose, by restriction of spore-production to the fertilised egg, from algal ancestors "which possessed archegonia as their female organs, and zoosporangia or aplanosporangia as asexual organs, with no regular alternation of generations, but with the power of bearing sporangia or sexual organs according to temporary conditions, just as is the case in so many green algæ." Assuming that the sporogonium of *Riccia* is primitive, it is of great interest as showing the first step in the progressive sterilisation of a simple spore-fruit formed by segmentation of the fertilised egg.

As already stated, the sporogonium does not reach a very high grade of development in the Marchantiales. This arrest of the sterilisation process is evidently correlated with the fact that in the Marchantiaceæ the stalked carpocephalum carries up the sporogonia into the air and thus renders unnecessary the development of a long sporogonial seta or of more elaborate mechanisms for spore dispersal, such as are found in the Jungermanniales. Only in the peculiar genus *Monoclea* is the capsule elevated on a long seta, as in the Jungermanniales; as already stated, this may be correlated with the extremely hygrophilous mode of life of this genus. In the Corsiniaceæ and Targioniaceæ there is no special means of raising the sporogonium above the general level of the thallus, but these plants do not grow in such moist situations, *Targionia* being in fact a xerophyte. Besides, there can be little doubt that the spores of many of the Marchantiales are dispersed by water rather than by air-currents. In this connexion, some interesting observations are made in a recent paper by Yeates (70), with reference to the distribution and dispersal of some British representatives of the Marchantiales and thalloid Jungermanniales; though it must be remembered that these groups are very poorly represented in Britain, and hence conclusions drawn from the scanty Hepatic flora of this country can hardly be applied to the liverworts as a whole. Still, Campbell notes the apparently complete absence of Hepaticæ from the new flora of Krakatau, as an indication that the spores of these plants are not generally well adapted for wind dispersal.

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(To be continued).

NOTES ON RECENT LITERATURE.

"Ancient Plants: being a simple account of the past vegetation of the Earth and of the recent important discoveries made in this realm of Nature Study." By Marie C. Stopes, D.Sc., Ph.D., F.L.S. Blackie & Son.

THE presentation of a general account of a subject such as Palæobotany, which shall be at once useful to students preparing for examination and intelligible to the non-specialist is a a task of exceptional difficulty. Dr. Marie C. Stopes tells us in the preface that her aim is to present "the most interesting discoveries and general conclusions of recent years," and to bring together the subject as a whole. The book is dedicated to college students, to the senior pupils of good schools . . . .", but especially, to "all those who take an interest in plant evolution, because it forms a thread in the web of life whose design they wish to trace." The non-scientific reader will find much in its brightly written pages which will assist him to form a fairly adequate idea as to the aims of those who study the plant records of the rocks, and as to the importance and fascination of the subject. To the student who has a general acquaintance with recent plants, the outline sketches of extinct types will serve as a stimulus to fill in details from other sources.

In Chapter II, following a brief introduction, the author gives a clear account of the commoner methods of preservation of plants as fossils. More use might have been made of amber as a convenient illustration of preservation by incrustation and petrifaction. Chapter III contains a good description of the manner of occurrence and probable origin of calcareous nodules in coal seams. In selecting as the heading of Chapter IV "The Seven Ages of Plant Life," Miss Stopes would seem to be influenced by an inherited devotion to Shakespeare, rather than by a determination to adhere strictly to scientific accuracy. The title is attractive, but misleading. Chapters V and VI include a brief account of plant-anatomy, with special reference to stages in evolution, and in illustration of the striking similarity between certain extinct and recent types. In these, as in other sections of the book, too much is attempted in a small space. To illustrate fossil genera differing more or less widely from existing forms, the reader is introduced in a chapter of ten pages to *Stigmaria*, *Lepidodendron*, *Medullosa*, as well as to *Lepidocarpon*, *Lagenostoma*, *Trigonocarpon* and other fossil seeds. In Chapter VIII a wholesome caution is given to those who look upon the relative abundance of fossil Amentiferæ as an indication of the primitive character of this division of Angiosperms. Chapters IX to XVIII deal with the main groups of ancient plants from the Gymnosperms to the Thallophytes. The descriptions, though necessarily condensed, are by no means dull, and many of the important points are well brought out.

In reference to the Bennettitales Miss Stopes writes: "This group is another of the jewels in the crown of fossil botany, for the whole of its structures have been reconstructed from the stones that hold all that remains of this once extensive and now extinct family of plants." The author's very fluent style is not always beyond reproach. Mutation is said to be "a cloak for an ignorance avowedly less mitigated than when we thought to have found a complete explanation of the causes of evolution in 'environment'." Similar sentences might be quoted to show how carefully the pen of a ready writer needs watching.

This sketch of ancient plants will we believe serve to arouse a wider interest in a department of knowledge the welfare of which the author has at heart, and in the advancement of which her own labours have already played an important part.

A.C.S.

"ON A LITTLE KNOWN TYPE OF VASCULAR STRUCTURE RE-DESCRIBED BY P. BERTRAND."

IN 1879 Renault (2) described under the name of *Lepidodendron Jutieri*, a fossil found under a dolmen in Alsatia and regarded by him as coming from the Culm; subsequently he modified the attribution of this form to the Lycopods, placing it with the Ferns and re-naming it *Adelophyton Jutieri* (3). M. Paul Bertrand has made a careful study of Renault's preparations and in 1907 he published an account correcting and extending the latter's observations (1). The striking peculiarities disclosed by Bertrand's elaborately accurate study of the only known example of *Adelophyton Jutieri* have, so far as the reviewer is aware, passed unnoticed in English botanical literature.

The fossil in question is a fragment of a stem; its phyllotaxy is $\frac{8}{21}$ and in a transverse section we find twenty-one foliar woody strands that have penetrated inwards for varying distances; the most internal one, *i.e.* that derived from the uppermost leaf of the cycle, has fused with a small circular internal strand. This internal strand is the *only other wood* found in the stem besides that of the decurrent traces. If we follow the sequence of events from below upwards we shall see that the internal strand describes a spiral corresponding to the $\frac{8}{21}$ phyllotaxy and appears to give rise successively to all the leaf traces. M. Bertrand speaks of this internal strand as a sympodium, formed by the fusion and prolongation of successive traces with a small compensation strand. Further he speaks of this internal strand as going to encounter the incoming woody strands, referring presumably to its spiral course; but from his figures it is clear that the wood of the incoming trace also passes inwards, separating from its mass of phloem, which, remaining more towards the periphery of the stem, forms with the other phloem masses a series of anatomosing strands similar to those found in recent Ferns. Moreover M. Bertrand repeatedly emphasizes the unique independence of phloem and xylem systems in this plant; he points out that though the two systems come into connection for the formation of traces, their independence could not well be greater. "It is," he says, "in fact absolutely necessary that the central sympodium should send a woody strand to each frond; in order to pass out this strand must make a hole in the phloem-tube; and it is almost obligatory that this opening should be produced precisely by the departure of the phloem of the same leaf-trace; ..... so that it is impossible to imagine a greater independence of the two systems without at the same time producing inextricable disorder in the arrangement of the stem."

As regards the histology of this remarkable plant the wood of the leaf-trace consists of a horse-shoe-shaped mass, normally oriented, *i.e.* with the concavity facing inwards, with five to seven groups of scalariform vessels on the inner edge; there is some evidence to show that as the trace passed out into the leaf it became concentric; though the course of the phloem strands is less peculiar than that of the xylem strands the protophloem is unique in that, according to M. Bertrand, it is distinctly central.

The most striking peculiarity of *Adelophyton* is perhaps the independence of xylem and phloem except in the leaf-traces, but the absence of any cauline xylem except the small internal compensation strand, and the central protophloem are highly peculiar. M. Bertrand remarks that the anastomosing phloem-strands, the structure of the individual phloem elements, the scalariform marking of the wood as well as the presence of highly developed "apolar" woody masses in the stem indicates a filicinean affinity; the horse-shoe-shaped trace seems to point in the same direction. M. Bertrand does not offer any suggestions as to the phylogeny of this peculiar type of vascular structure; the internal strand, however, is strongly reminiscent by its spiral course from leaf gap to leaf gap of the internal strands of polycyclic Ferns, especially of the single internal strand present in some of the simpler dicyclic forms. In the Ferns internal strands not uncommonly contribute to the leaf-traces, e.g., *Matonia pectinata*, *Pteris aquilina*, etc.; but in these cases they merely contribute to what appear to be, phylogenetically, later complications of the trace. But if we suppose that a reduction of xylem were to take place in a dicyclic form with a single internal strand and that such reduction were to be continued until all the purely cauline portions of the external (primitive) xylem cylinder had disappeared, it is obvious that it would be advantageous for the internal strand which usually comes into contact with the edge of the leaf gap, and which may contribute to the elaboration of the trace, to fuse with the incoming woody masses of the traces. Mr. Tansley has pointed out ". . . . that it is apparent that the primary stimulus to the development of an internal vascular system is the need for providing additional conducting or water storing tissue at the leaf gap when the departure of the trace largely diminishes the conducting capacity of the stele above that point" (4). It would seem that conduction to the traces would, in the absence of cauline portions of the external cylinder, be best brought about by a connection of trace and internal strand, and that in *Adelopyton Jutieri* this has been effected not by the bending out of the internal xylem-strand but by the the inward penetration of the *xylem only* of the trace. Such a course of evolution would involve a considerable reduction of the xylem of a dicyclic form. It is therefore interesting to note that M. Bertrand considers that the aeriferous tissue of this fossil denotes a very damp medium, such as might cause reduction of the xylem; he compares this tissue to that found in plants with the habit of a Mangrove. This aeriferous tissue is, however, associated with a certain amount of internal and external phloem.

I.M. P.B

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"HAYWARD'S BOTANISTS' POCKET-BOOK"; 13th ed., revised and enlarged by G. Claridge Druce, M.A., F.L.S.; London, G. Bell and Sons; 1909.

HAYWARD'S pocket flora has already had a useful career of almost thirty years; and Mr. Druce has performed an excellent service to British botanists in bringing this little book up-to-date so far as the circumstances would permit. The size and general arrangement of the book remain unaltered; but there are some necessary changes in the rearrangement of the families. For example, the Coniferæ no longer appear as Dicotyledons! The names of the families have been changed in some cases; thus, Lamiaceæ displaces Labiatæ, probably on the ground that it is the earliest name of the family ending in *-aceæ.*

In a book of this nature, abbreviations in the text are necessarily of very frequent occurrence; but a large number of them are not given in the introduction under the heading "Explanation of Abbreviations."

The greatest change is the introduction into the text of a large number of "elementary species" and varieties; and consequently the nature of the book has been radically altered. Doubtless there will be some differences of opinion as to the wisdom of this course; but for our part we are genuinely pleased that Mr. Druce has adopted it. For the first time, British botanists are in possession of an account—necessarily a brief one, in a pocket flora—of the *petites espèces* of their own country. The recent work of Mendel, de Vries, and Bateson has given to the study of these forms a much greater importance than before; and many modern field botanists have also adopted Jordan's point of view in the treatment of species. Bentham's condemnations fall unheeded on the ears of many of the field botanists of the present time.

There can be no doubt as to the author's thorough competence to discharge the task he set himself; and it may indeed be said that in the new "Hayward" we have an epitome of Mr. Druce's life-work. Until the book has been put to actual service in the field, it is, of course, impossible to say definitely whether or not the characters given for separating the closely allied species and varieties will prove adequate; but no serious doubts need be entertained that Mr. Druce has performed his work satisfactorily.

It is to be hoped that botanists who follow Mr. Druce in "splitting" species to such a great extent as is done in this book will not be satisfied with merely giving a name to the segregate forms. Few experiments have been made in this country on the permanence or otherwise of the characters of the indigenous "elementary species" when grown under definite conditions; and it is due to Mr. Druce to state that such work, owing to difficulties of determination of the critical forms, was nearly impossible before this edition of Hayward's pocket flora appeared. It is now possible for such work to be undertaken by any careful observer; and it is to be hoped that some British botanists will at once emulate the work of Bonnier and others in France.

We are glad to see that Mr. Druce follows the Vienna rules of nomenclature, though he was unable to avoid a veiled outburst against the list of generic "nomina conservanda" hastily adopted by the last International Congress. It is not unlikely that this list will be materially lengthened at the forthcoming Congress at Brussels; and doubtless we shall then hear more from Mr. Druce against the practice of conserving names in defiance of the principle of priority.

By following the rule retaining the earliest specific name (adopted by the Vienna Congress), many nomenclatorial changes are introduced; but the inconvenience caused by this rule (which appears to be now universally accepted) is minimized by the frequent addition of useful synonyms in the text.

Generally, it may be said that Hayward's Botanists' Pocket-Book has entered upon a new career of usefulness; and Mr. Druce is to be congratulated on his successful attempt to put new wine into an old bottle. C.E.M.

R. MADLEY, Steam Printer, 151, Whitfield Street, London, W.

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THE INTER-RELATIONSHIPS OF THE BRYOPHYTA,

By F. Cavers, D.Sc.

[Figs. 30—43.]

Phylogeny of the Marchantiales—*Continued.*

In considering the inter-relationships of the Marchantiales, the writer has adopted the view that the group forms an ascending series, starting from *Riccia* and culminating in *Marchantia*, though including some genera which show unmistakeable evidences of reduction in the gametophyte or the sporophyte.

The opposing view, according to which the Marchantiales show wholesale reduction, starting from a type like *Marchantia*, so that the genus *Riccia* represents not a primitive form but the lowest member in a descending series of reduction forms, gains considerable support from Goebel's recent study of the remarkable genus *Monoselenium*.[1] In 1849 there appeared in Griffith's "Posthumous Papers" (*Notulae ad plantas asiaticas*, Part 2) a brief diagnosis of a liverwort which has apparently been lost sight of entirely since that time, or which has been regarded as a *Cyathodium*. Goebel, who has re-discovered and thoroughly investigated the plant, shows that *Monoselenium tenerum* undoubtedly belongs to the Marchantiaceæ. The thallus has no trace whatever of air chambers, but it bears small ventral scales and tuberculate as well as smooth-walled rhizoids. The antheridia and archegonia are borne on receptacles and the plant is monœcious, the male receptacles standing just behind the female receptacles. The latter usually terminate the growth of a thallus-lobe, but are sometimes seated on the dorsal side of the thallus. The male receptacle is at first sessile on the thallus, but is sometimes raised later on a very short stalk, which has, however, no rhizoid-furrow. The receptacles of both kinds are of the "Composite" type. In the male receptacle the antheridia are developed in centrifugal order on the upper surface; the oldest antheridia occupy the centre of the receptacle, while the marginal tissue remains embryonic and gives rise to new antheridia, though there is apparently no definite arrangement in rows answering to a number of growing-points. The under side of the male receptacle bears scales and rhizoids. Immediately below and in front of the developing receptacle there appears an adventitious branch, which continues the forward growth of the thallus, so that the receptacle (which arises in the first instance as a terminal, *i.e.*, apical, structure) is shifted on to the dorsal side of the thallus. This continuation-branch then proceeds, either at once or after giving rise to a tract of thallus-tissue, to develop a female receptacle. The latter shows from four to ten groups of archegonia, each group being surrounded by an involucre and containing as many as twelve archegonia; the groups are separated by lobes bearing scales and rhizoids, which occur also on the lower part of each involucre. The ripe sporogonium strongly resembles that of the Corsiniaceæ, having a spherical capsule and a short "foot"; the capsule-wall consists of a single layer of unthickened cells—except at the apex where there is a cap composed of several layers, some of which have rudimentary thickening-fibres; the sterile cells mixed with the spores are short and retain their chlorophyll, and are either unthickened or show rudimentary annular or spiral fibres; the spores remain united in tetrads when ripe; the seta remains undeveloped, the capsule is not exserted from the involucre, and the spores escape merely by the irregular breaking-up of the capsule-wall.

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[1] Goebel, K. Archegoniatenstudien, XIII. *Monoselenium tenerum*, Griffith. Flora, 1910, pp. 43-97.

We may regard *Monoselenium* as a reduced form, the reduction extending to all the organs but being exhibited by the different organs in varying degrees. The thallus resembles that of *Monoclea* in having no trace of an air-chamber zone, but the ventral scales, instead of being reduced to unicellular or filamentous gum-papillæ, resemble rather those of *Dumortiera* or *Cyathodium*—which, as we have seen, are certainly reduced forms. In the structure of the sporogonium, *Monoselenium* forms a perfect connecting-link between the genera *Corsinia* and *Boschia*; sterile cells resembling those of *Corsinia*, *Sphærocarpus*, and *Riella*, occur in the same capsule with rudimentary elaters like those of *Boschia*. But the most remarkable feature of *Monoselenium* is Goebel's discovery that sexual receptacles of the "Composite" type may become shifted on to the dorsal side of the thallus, so as to occupy the same position as the archegoniophores of *Clevea* and *Plagiochasma*. The writer has already suggested that "the carpocephala of all the Marchantiaceæ, except *Clevea* and *Plagiochasma*, represent branch-systems." This suggestion was based on the fact that several archegonia were found to be produced from each growing-point in the receptacles of various genera (*Sauteria*, *Peltolepis*, *Grimaldia*, *Neesiella*, *Reboulia*, *Fimbriaria*) in which the archegonia were formerly regarded as occurring singly in each involucre. Goebel's observations on *Monoselenium* not only support this suggestion, but show that there is no need to exclude *Clevea* and *Plagiochasma* from the general interpretation of the archegoniophore as representing invariably a branch-system. It is clear that a "Composite" receptacle, in which the sexual organs are developed in centrifugal order from several growing-points and which is therefore a branch-system, need not necessarily terminate the growth of the thallus, but may come to occupy the sameposition as the "dorsal outgrowth" type of receptacle which Leitgeb regarded as contrasting strongly with the "branch-system" type.

Goebel proceeds to elaborate the view that those members of the Marchantiales in which the sexual organs are borne in receptacles seated on the upper side of the thallus, or in which these organs are borne dorsally but not grouped into receptacles at all, are reduced and not primitive forms. He also suggests that the *Riccia* sporogonium, in which sterilisation is limited to a single peripheral layer of cells is not a primitive type of sporophyte, but is the lowest term in a descending series of forms in which the elaters become reduced to short sterile cells and finally are not developed at all. But further discussion of the wider questions raised by the study of the Marchantiales may be deferred until a later stage. As regards the systematic position of *Monoselenium*, it is by no means easy to determine the affinities of this aberrant and greatly reduced genus; Goebel shows that its archegoniophore differs in several apparently essential respects from that of *Dumortiera*, while the far-reaching reduction of the sporogonium sets it apart from every other known Marchantiaceous genus.

It is interesting to note that androgynous receptacles, in which antheridia and archegonia may even occur intermingled, as well as occupying different portions of the same receptacle, occur in *Monoselenium*. In this peculiarity the genus resembles *Dumortiera*, though androgynous receptacles occur also in *Preissia* and have recently been described by Cutting[1] in a species of *Marchantia*. The occurrence of these "abnormal" receptacles is of interest from various points of view; for one thing, they demonstrate the homology which exists between the male and female receptacles throughout the Marchantiaceæ, and which could otherwise be inferred only from the facts of comparative morphology.

[1] Cutting, E. M. "On Androgynous Receptacles in *Marchantia*." Annals of Botany, vol. 24, 1910, pp. 349-357.

III. ANACROGYNOUS JUNGERMANNIALES.

The Jungermanniales were divided by Leitgeb (40, 41) into a lower series (Anacrogynæ) and a higher series (Acrogynæ), for which Underwood (70) proposed the terms Metzgeriaceæ and Jungermanniaceæ respectively. The Acrogynæ owe their name to the fact that the apical cell of the main axis or of a branch eventually becomes an archegonium, so that apical growth is arrested by the production of a group of archegonia. It is also characteristic of the Acrogynæ that at least the sexual branches, and in the vast majority of cases the entire plant-bodies, are differentiated into stems and leaves, and that the young leaf divides primarily by a radial wall into two cells which in many cases grow out independently for a longer or shorter time and frequently give rise to two deeply separated lobes. Many of the Anacrogynæ also show differentiation into stem and leaves, but the leaf-primordium never shows the initial division into two lobes; and in all the forms placed here, excepting the Calobryaceæ, the archegonia are borne on the upper side of the thallus or of the stem, the apical growth of which is therefore not necessarily arrested by the development of these organs.

This two-fold division of the Jungermanniales is largely an artificial one, and as a matter of fact we find among the Anacrogynæ a series of types in which the development of the archegonia becomes, as it were, shifted nearer and nearer to the apex, while we have also a series of striking parallel developments, along independent lines, leading to the differentiation of a leafy shoot from a simple thalloid plant-body. The Jungermanniales form a single phylum, the boundaries between the systematic families are in most cases badly defined, and probably in no other group of plants do we find such striking and abundant examples of parallelism or homoplasy.

The general characters of the Jungermanniales, as contrasted with the Marchantiales, have already been enumerated, and we have seen that the two phyla are connected by the synthetic group of the Sphærocarpales, which combine several of the distinctive characters of the Jungermanniales and Marchantiales, though on the whole probably standing nearer to the latter, and at the same time presenting peculiar features of their own.

The Anacrogynæ may be divided into four families, whose inter-relationships will be discussed later. This division differs somewhat from that adopted by Schiffner (54); the genus *Monoclea* has, in this series of articles, been transferred to the Marchantiales, while two genera discovered recently (*Makinoa* and *Cavicularia*) are here dealt with, and some minor changes in classification are suggested, such as the splitting up of *Pallavicinia* into two genera (*Blyttia* and *Mörekia*) and the restoration of the old division of *Hymenophytum* into two genera (*Podomitrium* and *Umbraculum*).

ANEURACEÆ.

This family (Schiffner's Metzgerioideæ) contains four genera—*Aneura* with over 150 species, *Metzgeria* with about 70, *Podomitrium* and *Umbraculum* (united by many writers into a single genus, *Hymenophyton*) with 2 species each. One of the most characteristic features common to these four genera is the restriction of the antheridia and archegonia to short special branches, which arise from the margin of the thallus in *Aneura*, but are ventral in origin in the other genera.

The genus *Aneura* received its name from the fact that in the European species the thallus differs from that of *Metzgeria* in not being sharply differentiated into a cylindrical mid-rib and a thin single-layered wing on either side of it, but in reality more than half the species of *Aneura* now known do show this differentiation, which is present in all the species of the other three genera. In several of these winged and often epiphytic species of *Aneura* there is considerable differentiation of the thallus branches.[1] In *A. bogotensis* the branches arising on one side of the creeping axis remain short and cylindrical and become attached to the substratum, while those on the other side of the axis branch repeatedly and give rise to broad flattened assimilating organs. In *A. eriocaula* and *A. fucoides* the lower branches serve as organs of attachment and, like the main axis itself, remain cylindrical, while the upper branches are erect, spreading, flattened and differentiated into mid-rib and wings. In other species there are various adaptations for the retention of water by capillarity. In *A. hymenophylloides* the branches have strongly incurved margins, forming water-sacs. In *A. fuegiensis* the same purpose is served by longitudinal lamellæ which project from the lower surface of the thallus. The genus is of great interest as showing the possibilities of the simple thallus,

[1] Several of these species are figured by Goebel (17).

with its forking or (more frequently) monopodial and pinnate branching, in the way of that differentiation into axis and leaves which has arisen repeatedly along independent lines among the lower Jungermanniales.

Many of the species of *Metzgeria* are epiphytes, and among

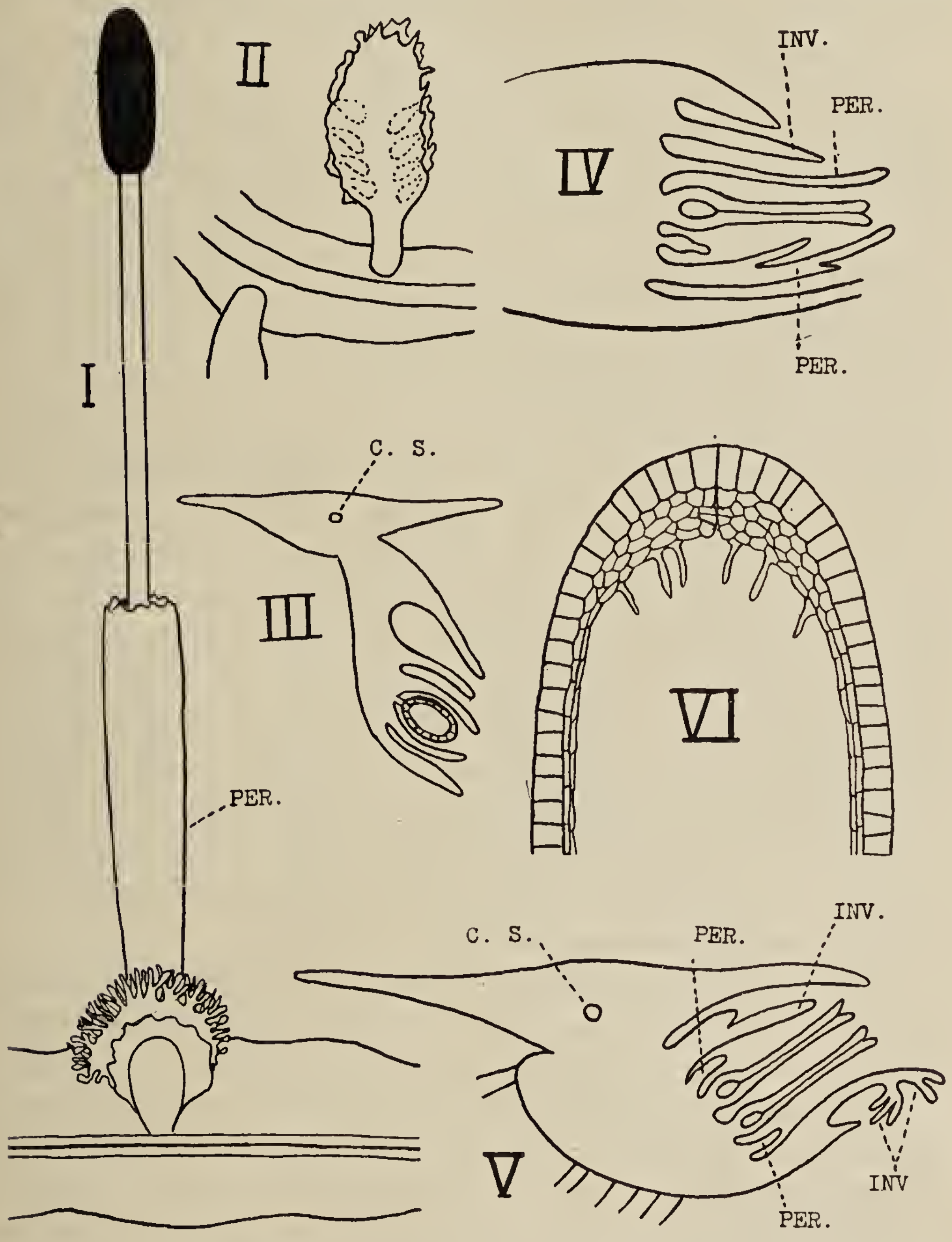


Fig. 30. *Podomitrium (Hymenophytum) phyllanthus.*—I, Part of a female plant from below, showing a female branch with ripe sporogonium ; II, Part of a male plant, from below, showing two antheridial branches ; III, Transverse section of a male plant traversing an antheridial branch ; IV, Longitudinal section of an archegonial branch, after fertilisation, showing the developing perianth within the involucre ; V, Similar section showing the appearance of the perianth before fertilisation ; VI, Upper part of a longitudinal section through a ripe capsule, showing the apical thickening of the capsule-wall. *c.s.*, conducting strand ; *inv.*, involucre ; *per.* perianth.

these there is an interesting form, *M. saccata*, which bears curious water-sacs. Each sac is formed by the margin of the wing becoming in certain places rolled over towards the underside and then by active superficial growth converted into an ovoid structure with its opening directed towards the lower side of the mid-rib; from the convex outer surface of the sac rhizoids frequently grow out.

A third line of differentiation of the thallus is seen in *Umbraculum*. In the allied genus *Podomitrium*, e.g. *P.* (*Hymenophytum*) *phyllanthus* (Fig. 30), ordinary apical branching occurs, but numerous branches arise from the mid-rib on the underside of the thallus. The basal portion of each branch is nearly cylindrical, but the distal portion develops on either side a broad wing, which frequently narrows again and becomes obsolete at the end of the branch; the rhizoids spring chiefly from the stalk-like basal portion. In *Umbraculum*, e.g., *U.* (*Hymenophytum*) *flabellatum*, however, the creeping, wingless rhizome-like basal portion, to which the rhizoids are confined, gives off erect branches which are at first cylindrical, but towards the top become winged and then undergo repeated dichotomy to form a fan-like assimilating branch-system (Fig. 31). Goebel (26) has shown that when this highly differentiated plant is grown in moist air and feeble light the fan-like shoots may produce rhizoids and their growing-points may grow out to form wingless runners or rhizomes. The axis or mid-rib in *Podomitrium* and *Umbraculum* is traversed by a strand of narrow elongated cells with thick walls which bear slit-like pits. The axial bundle of a ventral branch is not continuous with that of the parent-axis, but is separated from it by a zone of thin-walled cells, hence these ventral branches readily become detached.

In all three genera the sexual organs are borne on special short branches. In *Aneura* these arise from the margin of the thallus and are merely lateral branches whose growth in length is arrested by the formation of the antheridia or archegonia, but in the other genera these organs are confined to short ventral branches arising from the sides of the mid-rib. The antheridia are either sunk in cavities in the tissue of the male branch, or are covered by the inrolled margins of the branch, or protected in both these ways. In *Podomitrium*, the male branch has a cylindrical stalk and an expanded distal antheridium-bearing portion (Fig. 30, II.); in *Metzgeria*, its margins are rolled up so as to form a sac; in *Umbraculum*, the male branch is reduced to a sessile cushion-like outgrowth of the mid-rib (Fig. 31). There is thus a gradual reduction in the structure of the male branch in the four genera, reaching its limits in *Umbraculum*.

In *Aneura* and *Metzgeria* the female branches are very much

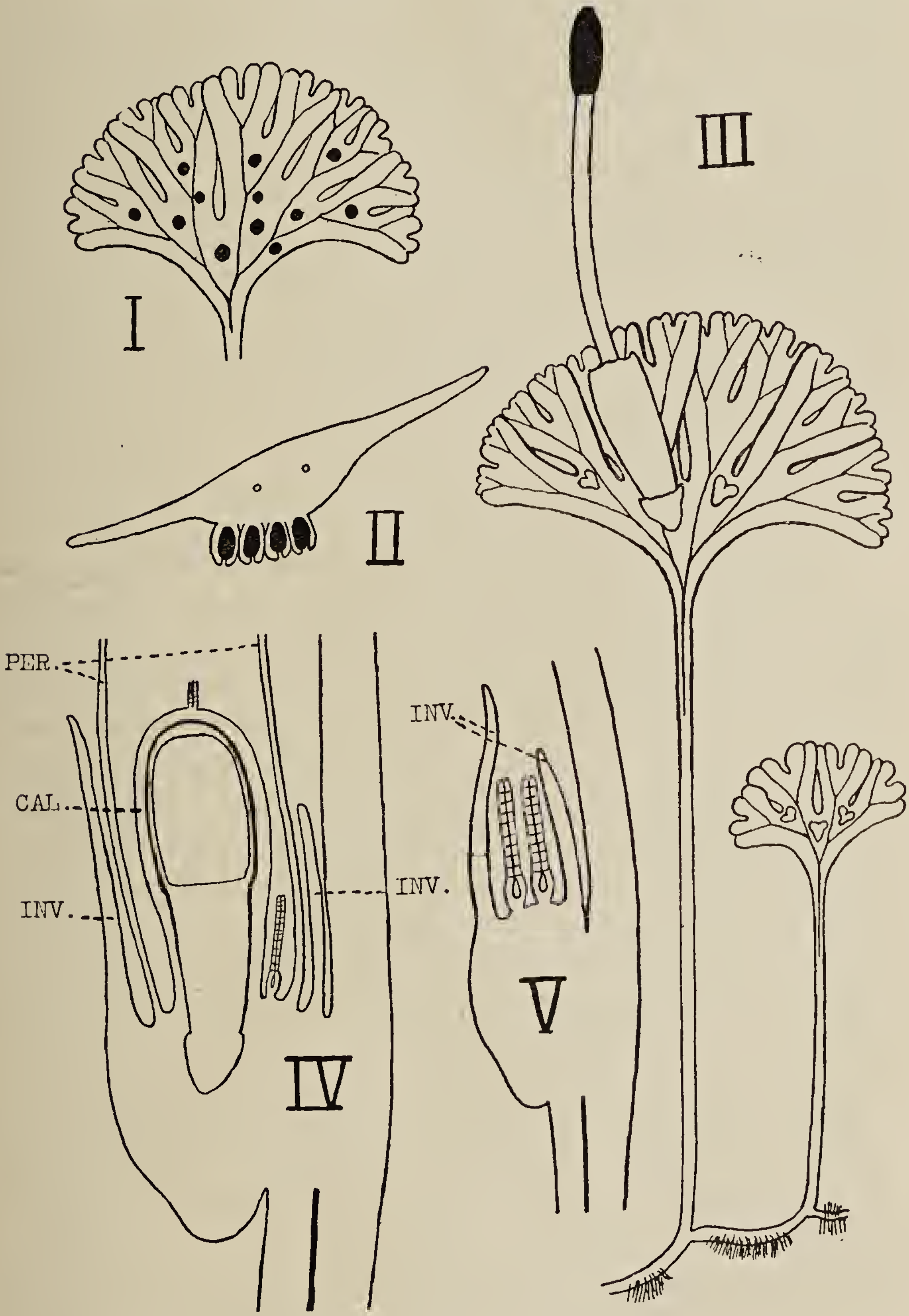


Fig. 31. *Umbraculum (Hymenophytum) flabellatum.* I, Part of a male plant, from below, showing the antheridial branches (diagrammatic); II, Cross section of a male plant, showing the antheridia; III, Part of a female plant, with archegonial branches and a sporogonium; IV, Longitudinal section of an archegonial branch with a nearly ripe sporogonium; V, Similar section of a branch with unfertilised archegonia. *cal.*, calyptra; *inv.*, involucre *per.*, perianth.

like the male branches. In *Podomitrium* the female branch is short but differentiated into a cylindrical portion which bears a narrow wing; on the expanded end of the branch are developed the archegonia, surrounded by a collar-like envelope (involucre) with fringed margins (Fig. 30, I.) In *Umbraculum* the wing of the female branch is more fully developed, and the involucre is reduced to a scale instead of forming a bell-like sheath (Fig. 31, III.) In *Aneura* and *Metzgeria*, the sporogonium is protected until ripe by the calyptra, which is a thick fleshy structure, often bearing on its surface the unfertilised archegonia. In *Podomitrium* and *Umbraculum* there arises within the involucre a second sheath (perianth) surrounding the archegonia; in the former genus the perianth is laid down before fertilisation occurs, in the form of a few scales arranged in a ring, the scales being later carried up by active growth of the tissue at their base (Fig. 30, IV., V.), but in *Umbraculum* the perianth arises after fertilisation in the form of a ring-like outgrowth of the tissue surrounding the archegonia (Fig. 31, IV.)

In all four genera, the sporogonium has a well-developed seta which rapidly elongates when the capsule is mature and thrusts the latter through the calyptra, the capsule then opening, typically, by four valves extending from apex to base. The early stages in the embryogeny have only been studied in *Aneura*, and the following account is based upon the writer's examination of the sporogonia of *A. pinguis* and *A. latifrons*. The lower (hypobasal) cell formed by the first transverse division of the oospore either undergoes no further development or divides by a few walls, chiefly transverse, to form a short appendage; hence practically the whole sporogonium (capsule, seta, foot) is formed from the upper (epibasal) half of the segmented oospore, the foot arising as a club-like swelling of the lower end of the seta. The epibasal cell first divides, as a rule, by a transverse wall, which separates the capsule from the seta. Then intersecting vertical divisions set in, together with further transverse divisions in both the upper and lower epibasal cells, so that there are now several superposed tiers consisting each of four cells. Up to this point, *Aneura* follows what is probably, with slight differences in detail, the development characteristic of all the Jungermanniales. In *Aneura*, as in other Anacrogynæ which have been investigated, the capsule is derived from the uppermost tier of four cells, but in many Acrogynæ one or more of the tiers formed in the lower epibasal series may contribute to the formation of the capsule besides forming the seta. In both the capsule- and the seta-forming tiers, divisions next occur which cut off four axial rows of cells (the endothecium) from a layer of outer cells (the amphithecium). The further development of the *Aneura* capsule, from this stage onwards, has been well described by Goebel (23) and by Bower (4). The amphithecium gives rise to the capsule-wall, which at a very early stage becomes two-layered and remains so throughout its development; the whole of the rest of the capsule is derived from the four primary endothecial cells. The tissue formed by the early divisions of the endothecium is uniform, but this tissue soon becomes differentiated into two portions, which Goebel characterises as "independent meristems." The peripheral cells, forming a U-shaped layer or band in a longitudinal section of the capsule, divide rapidly and contain dense protoplasm, with chloroplasts but no starch; the central cells, continuous above with the apical portion of the capsule-wall, undergo relatively few divisions, are more transparent and contain starch, but no chlorophyll. As Bower has clearly shown, the cells produced by the inner portion of the peripheral band, as development proceeds, assume the characters of the central cell-group, so that the latter becomes more extensive, and the densely-staining peripheral region becomes reduced to a thin peripheral fringe around the sides and base of the large central tissue. The peripheral fringe, which produces the spores and free elaters and to which the term archesporium might therefore be restricted, now begins to grow actively and becomes more sharply marked off from the sterile columella, which hangs downwards into the cavity of the capsule. As the development of the capsule proceeds, the size of the sterile columella, as compared with the capsule as a whole, diminishes, so that in a ripe capsule of *A. pinguis* the columella extends only about one-third the distance from apex to base of the capsule. The columella probably serves to nourish the fertile tissue during the early development of the capsule, since its cells contain starch, but as the capsule ripens the starch disappears from this sterile tissue and the cells become elongated and acquire ring-like fibrous thickenings. Ordinary free elaters, pointed at each end, are developed amongst the spores, but from the surface of the columella (which is also termed the "elaterophore") there grow out elater-like cells ("fixed elaters") which project into the mass of spores and free elaters.

When the capsule is pushed up through the calyptra by the elongation of the seta, the capsule-wall and also the columella or "elaterophore" split into four parts, along lines of thin-walled cells which are recognisable (both in the capsule-wall and the columella) before the capsule is ripe. Thus each of the four valves of the capsule-wall has attached to its tip a quarter of the columella, with its tuft of fixed elaters, and as the four valves bend outwards each of the four masses of spores and elaters moves into a vertical position on the valve, and the spores, together with the loose or free elaters, are actively flicked outwards. Hence the columella, after splitting into quarters, brings about the active dispersal of the spores.

Metzgeria differs from the other three genera in having spherical instead of ovoid or cylindrical capsules, but the structure is very much the same as in *Aneura*; the elaterophore is not quite so well developed, and its cells have only here and there irregular thickenings on their walls, instead of the well developed half-rings found in the larger elaterophore of *Aneura*.

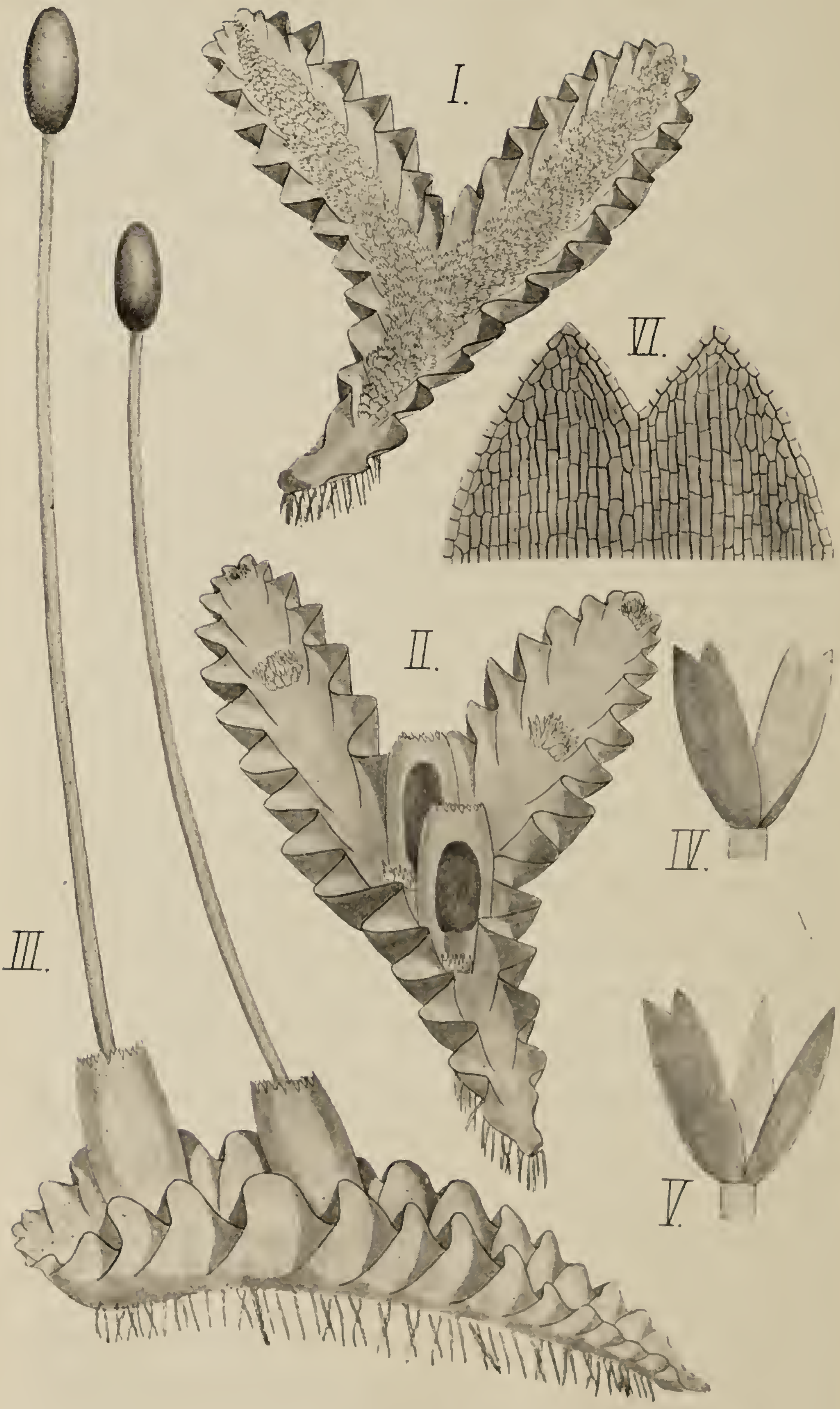
In *Podomitrium* and *Umbraculum* the capsule-wall consists of an outer layer of large nearly cubical cells, and one or two inner layers of elongated and flattened cells. According to Andreas (1), these inner cells are continuous with the apical pad or cap, lying below the layer of large outer cells, at the top of the capsule, and Goebel (26) therefore distinguishes this cap from the columella of *Aneura* and *Metzgeria* as being of different origin, comparing it to the apical thickening of the capsule-wall found in various Marchantiales. In the latter group, however, the apical cap cannot always be interpreted as arising by periclinal division of the otherwise single-layered capsule-wall, and it is not easy to determine the exact origin of the cap. In *Fegatella* and *Reboulia*, according to the writer's investigation of these genera (10, 11), this cap is derived from the archesporium, the apical portion of which exhibits sterilisation comparable to that seen in *Aneura*. In any case, however, the capsule-wall in Marchantiales is not differentiated until a relatively late stage; that is, the separation of the archesporium is not determined by the first periclinal divisions in the young capsule. In *Umbraculum* (*Hymenophytum*) *flabellatum* the cap, or elaterophore, splits into four portions, as in *Aneura* and *Metzgeria*, one remaining attached to the tip of each valve of the dehisced capsule and bearing a number of fixed elaters. In *Podomitrium* (*Hymenophytum*) *phyllanthus*, however, the capsule dehisces by from two to four slits, but these do not extend to the apex, where the valves are coherent. In *Umbraculum* the large outer cells of the capsule-wall have localised but indefinite band-like thickenings on the radial cell walls, but in *Podomitrium* these cells are uniformly thickened and bear no definite fibres; in both genera there arise from the bottom of the capsule cavity isolated fixed elaters of varying form, some being short and without fibrous thickenings, others long and elater-like.

In *Aneura* the developing sporogonium is protected by a massive and fleshy calyptra formed by vigorous growth of the tissue of the female branch; this active growth extends to the tissue underlying the fertilised egg, where a projecting bulbous mass is formed, bearing rhizoids. The calyptra carries up the scales which grow out around or among the archegonia, and usually also the unfertilised archegonia themselves. In *Metzgeria* the calyptra is not so massive, and is formed chiefly from the venter of the fertilised archegonium.

In the Aneuraceæ, asexual reproduction is effected in various ways. The simplest is the separation of ordinary branches by the dying away of the old portions of the thallus; in *Podomitrium* and *Umbraculum* the severance of the branches from the parent axis is facilitated by the fact that the strand of thick-walled cells in the ventral branch is not continuous with that in the parent stem.

The asexual reproduction of *Metzgeria* by means of gemmæ has recently been investigated by Evans (15), who has shown that each of these bodies (consisting usually of a single layer of cells) arises from a single cell of the parent thallus, either from a cell of the wing or from one of the cortical cells of the mid-rib. The superficial cell about to produce a gemma projects beyond its neighbours; the outer wall of the cell is ruptured, but the protruding protoplast becomes covered by a layer of gelatinous material which probably represents a modification of the inner part of the original outer wall and which is deposited prior to the rupture of the wall. The projecting cell thus formed, either with or without a preliminary division into a lower cell which does not enter into the formation of the actual gemma, usually undergoes at once divisions which cut out a two-sided apical cell; in some cases the gemma has two growing-points from the earliest stages of its development. The details vary greatly in different species, as shown by Evans.

In several species of *Aneura*, gemmæ are formed in a somewhat different manner. The contents of a superficial cell of the thallus separate from the wall, and the rounded-off protoplast acquires a cell-wall and divides into two cells. The two-celled gemma escapes by rupture of the free outer wall of the mother-cell. As compared with *Metzgeria*, the further development of the gemma in *Aneura* is deferred until after the gemma is set free.



(For description see next page).

Fig. 32. *Mörckia flotowiana.* I, Male plant, from above, showing the broad midrib covered by toothed scales (male bracts), each of which forms a hood over an antheridium, ×5. II, Female plant, from above. Six archegonial groups are seen. In the four younger groups the archegonia are surrounded by the involucral leaves (female bracts), the perianth not yet being developed; in the two older groups the perianth is represented as being transparent, to show the half-ripe sporogonium within it, ×5. III, Female plant, bearing two ripe sporogonia; in each case the seta has become elongated, carrying up the capsule, which has not yet dehisced, ×5. IV and V, Ripe capsules, showing different modes of dehiscence, ×8. VI, Upper portion of one of the valves of a capsule, ×40.

BLYTTIACEÆ.

Under this name it is proposed here to designate a family, agreeing in part with Spruce's family "Leptotheceæ," in which Schiffner includes three genera—*Pallavicinia*, *Symphyogyna*, and *Monoclea*. The first-named genus should, however, be split into the two genera *Blyttia* and *Mörckia*; while *Monoclea* has been removed to the Marchantiales. The recently discovered genus *Makinoa* is probably best placed here, so that our family Blyttiaceæ includes the four genera *Blyttia*, *Mörckia*, *Symphyogyna*, and *Makinoa*. The name Leptotheceæ was suggested originally by Spruce (60) to include the three genera placed in it by Schiffner and also the genus *Calobryum*, on account of the absence of ring-fibres from the cells of the capsule-wall and the incomplete separation of the capsule-valves at dehiscence.

The Blyttiaceæ are distinguished from the Aneuraceæ chiefly by the fact that the sexual organs are born on the upper side of the ordinary thallus and not on special short branches. The four genera of Blyttiaceæ differ in so many respects that it will be convenient to describe them separately.

In *Blyttia*, the thallus is differentiated into a cylindrical midrib and a single-layered wing on either side. In twenty of the thirty known species, the whole thallus is attached to the substratum. In some cases, e.g., *B. Lyellii*, the margin of the wing is entire, but in several species belonging to this "Repentes" section of the genus, e.g., *B. longispina*, *B. xiphioides*, the margin bears regular appendages which, as shown by Goebel (22, 24), may be regarded as representing leaves, since they are formed with great regularity at the growing-point, which it is their primary function to protect. In the remaining species, forming the section "Erectæ" or "Dendroides," *e.g.*, in *B. decipiens* which was fully investigated by Farmer (16), the thallus consists of a creeping cylindrical basal portion, consisting of the midrib alone, and an erect distal winged portion which undergoes repeated dichotomy, the branches spreading out like a fan—exactly as in *Umbraculum.* The midrib is traversed by an axial strand of pitted cells, and Tansley (68) showed that in *B. Lyellii* eosin solution passes along this strand more rapidly than through the surrounding tissue of the midrib, so that we have here a rudimentary conducting strand. The antheridia are borne in two rows along the midrib on the upper side of the thallus, each antheridium being spherical, shortly-stalked,

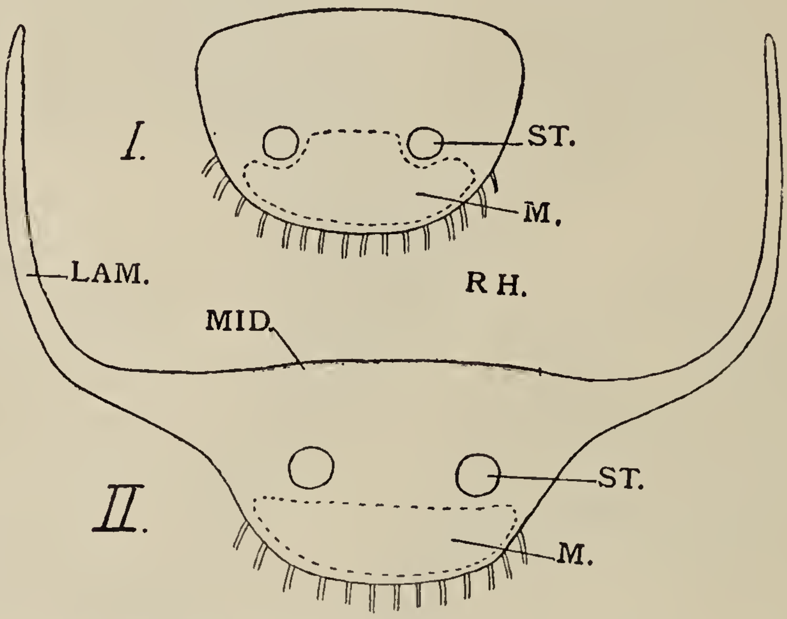


Fig. 33. *Mörckia flotowiana.* I, Transverse section through base of plant. II, Similar section taken further forwards. *st.*, conducting strands of midrib; *m.*, mycorhizal zone; *rh.*, rhizoids; *lam.*, lamina or wing of thallus; *mid.*, midrib. ×25.

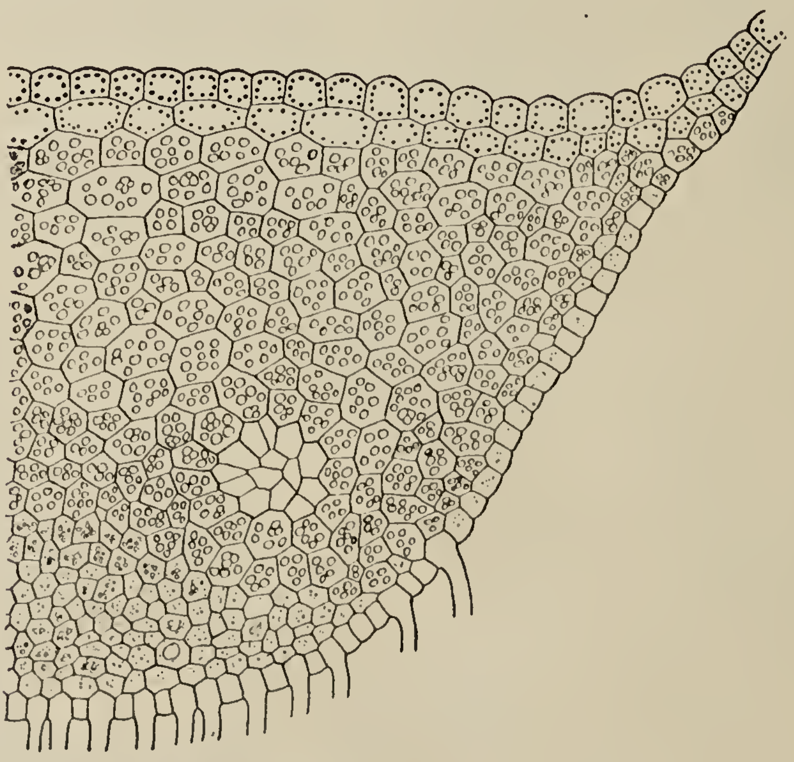


Fig. 34. *Mörckia flotowiana.* Part of Fig. 33, II, ×70.

and covered from behind by a hood-like scale. The archegonial groups, also borne dorsally, are each surrounded by a short cupule-like involucre formed from a series of toothed scales and by a much longer perianth which is laid down before fertilisation occurs, exactly as in *Podomitrium* ; within the perianth is the calyptra, which is about the same length or a little longer and which usually bears near the top the unfertilised archegonia. The capsule has much the same structure as in *Podomitrium*, and it usually opens by two to four slits, the valves generally remaining attached at the top, where there is a cap-like mass of tissue.

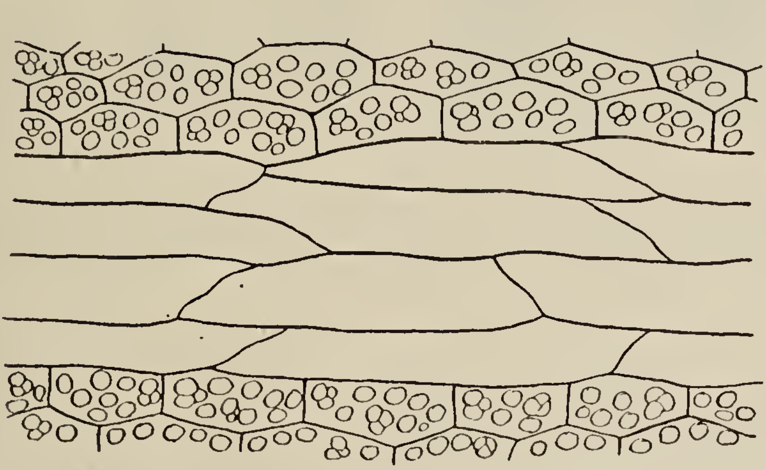


Fig. 35. *Mörckia flotowiana.* Part of a longitudinal section of the midrib, traversing one of the conducting strands. On either side of the elongated hyaline strand-cells are the cortical cells, packed with starch grains. ×180.

In *Mörckia*, the thallus is always creeping, as in the "Repentes" section of *Blyttia*, with a broader midrib and less sharply defined wings, the latter being frequently wavy, (Fig. 32) but never showing incipient differentiation of leaves. In *M. Flotowiana* the midrib contains two strands of elongated cells (Figs. 33-35), but these are of much simpler structure than the strands of *Blyttia*, *Symphyogyna*, *Podomitrium*, and *Umbraculum*. There are small filamentous appendages on the lower side of the thallus, especially at the growing point (Fig. 36), and in *M. Blyttii* numerous small leaf-like appendages are borne on the *upper* surface along the midrib. These appendages are similar to the scales which in all species of *Blyttia* and *Mörckia* cover the antheridia. In *Mörckia* the antheridia are sometimes developed in more than two rows, and the scales covering them are more or less fused together, so that the antheridia appear to be sunk in chambers (Fig. 36) in the upper tissue of the thallus. The involucre and perianth in *Mörckia* resemble the corresponding structures in *Blyttia*, but the capsule-wall has from three to five layers of small cells within the outer layer of large cells (Fig. 37).

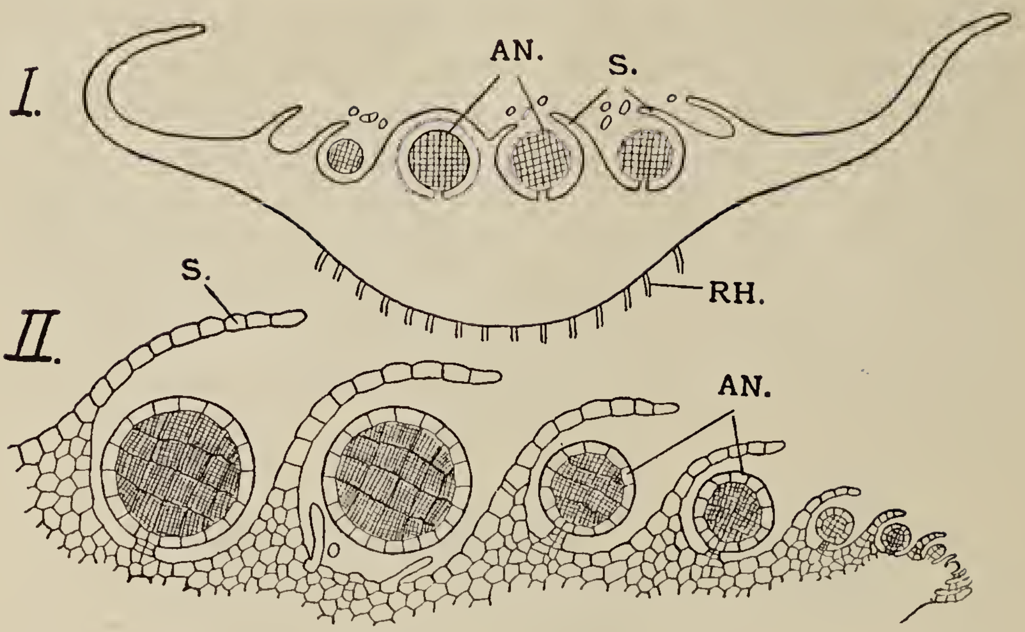


Fig. 36. *Mörckia flotowiana.* Transverse (I) and longitudinal (II) sections of a male plant showing the antheridia (*an.*) and the scales (*s.*) covering them; *rh.*, rhizoids. I × 25, II × 70.

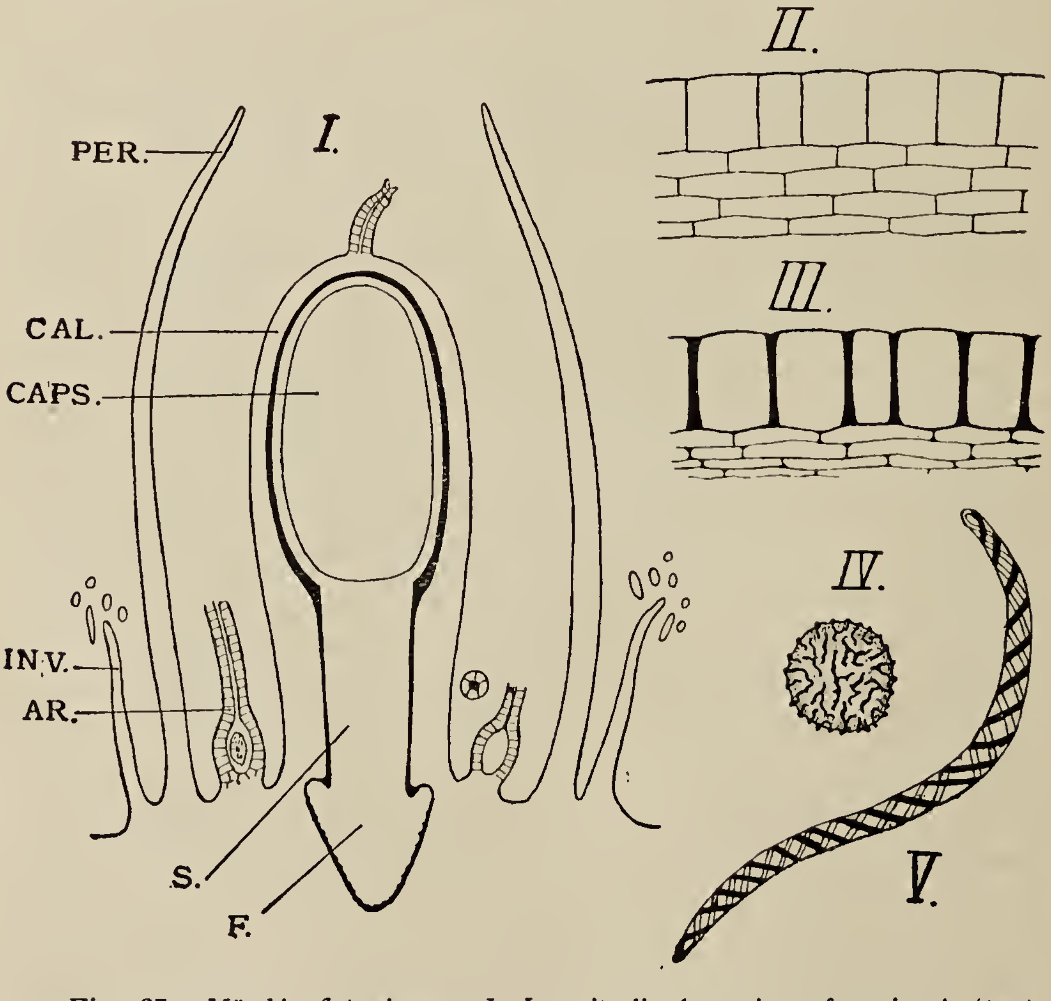


Fig. 37. *Mörckia flotowiana.* I, Longitudinal section of perianth (*per.*) with a nearly ripe sporogonium, enclosed in its calyptra (*cal.*) *caps.*, capsule; *inv.*, involucre; *ar.*, unfertilised archegonium; *s.*, seta, and *f.*, foot of sporogonium. II, Part of transverse section through wall of young capsule. III, similar section of mature capsule. IV, Spore. V, Elater. I, × 25; II and III, × 180; IV and V, × 250.

The capsule-wall splits along more or fewer of the four dehiscence lines laid down previously, hence the number of valves varies from two to four; the valves do not cohere at the top, as a rule.

Symphyogyna (Fig. 38) differs from *Blyttia* and *Mörckia* in having no perianth; the calyptra, instead of being thin as in these genera, is massive and bears on its upper portion the unfertilised archegonia; the involucre consists of a single scale. In practically every other respect, however, *Symphyogyna* shows an extraordinarily close resemblance to *Blyttia*, and it is very difficult to distinguish between sterile plants of the two genera. Moreover, the species of

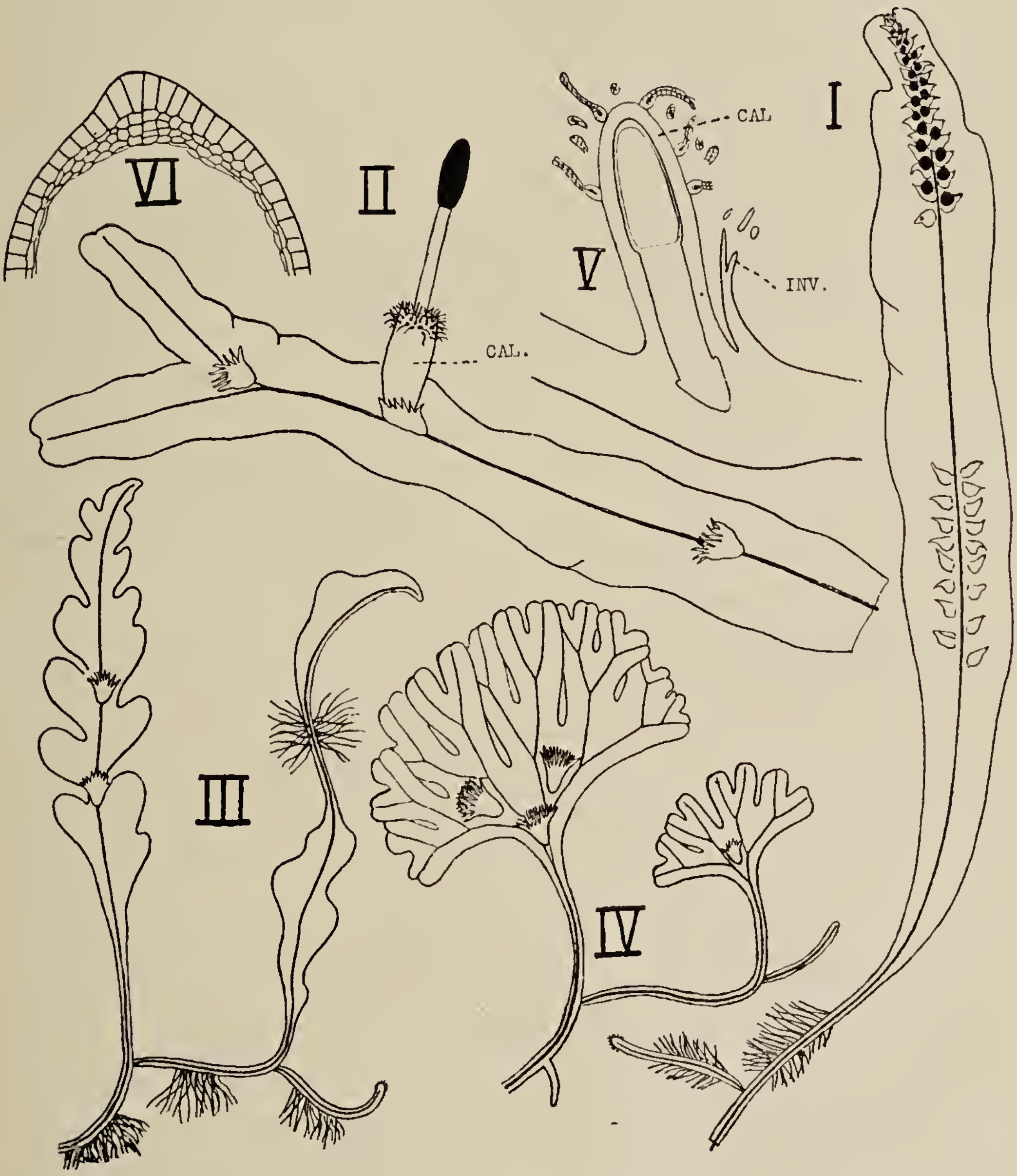


Fig. 38. *Symphyogyna*. I, A male plant of *S. brasiliensis*. II, a fruiting female plant of the same species. III, A female plant of *S. Brongniartii*. IV, A female plant of *S. hymenophyllum*. V, Longitudinal section of female branch of *S. brasiliensis*, showing a developing sporogonium. VI, Longitudinal section of upper part of capsule of *S. brasiliensis*. *cal.*, calyptra; *inv.*, involucre.

Symphyogyna fall into two sections, corresponding exactly to the "Repentes" and "Dendroideæ" sections of *Blyttia*. Among the creeping species, some have the margin of the wing entire; in others there are marginal teeth; in others again, the wing is sinuately lobed; and in some species the wing may be absent from one side of the midrib, though present on the other side. The "Dendroid" species have a basal creeping portion and an erect portion consisting of fan-like dichotomising branches, like the corresponding species of *Blyttia*. If we regard *Podomitrium* and *Umbraculum* as forming sections or sub-genera of the genus *Hymenophytum*, we have a striking parallelism between the three genera, each having flat creeping species and erect dendroid species. This parallelism was pointed out by Farmer in his memoir on *Pallavicinia (Blyttia) decipiens* (16). In *Symphyogyna*, as in *Blyttia*, the midrib is traversed by an axial strand of lignified and pitted cells; in some species there are two or even three of these strands (29). The capsule has the same structure as in *Blyttia*; after being thrust through the thick calyptra which envelops it, the capsule opens by valves which remain coherent at the top.

In the Japanese genus *Makinoa*, which was originally described by Stephani (65) as a *Pellia* but later recognised as an independent genus, and described by Miyake (51) and by Schiffner (59), the thallus is very similar to that of *Mörckia*, having a wavy margin and filamentous ventral scales. The antheridia are collected into a definite receptacle, occupying a depression on the upper side of the thallus, and each antheridium is sunk in a chamber which is open above and is separated from the neighbouring chambers by a partition two cells thick. The archegonial group is covered by a lobed hood-like scale, as in *Symphyogyna*, and the young sporogonium is protected by a massive calyptra formed by outgrowth of the thallus tissue and bearing on its surface the unfertilised archegonia, as in *Symphyogyna* and *Aneura*. The ellipsoid capsule opens, as a rule, by two valves which may remain coherent at the top. The capsule-wall is two-layered, the outer cells being large and having thickening bands on the radial cell-walls, while the inner cells are narrow and thin-walled; at the apex of the capsule there is a cap consisting of three or four layers of cubical cells, and to this cap are attached long elater-like filaments, differing from the ordinary free elaters in having no fibrous thickenings.

CODONIACEÆ.

This family is distinguished from the Blyttiaceæ chiefly by the characters of the capsule, which is spherical (ovoid in *Blasia*) and when ripe, dehisces by four valves extending from apex to base (except *Fossombronia* and *Petalophyllum*, where the wall breaks up into irregular plates). The capsule-wall consists typically of two layers of cells (four in *Blasia* and *Treubia*), well-developed fibrous thickenings being usually present in either the outer or the inner cells, or in both. There is usually a basal columella or elaterophore but sometimes this is represented only by a few elongated elater-like cells at the base of the capsule-cavity. In addition to the calyptra, there is usually a tubular envelope around the sporogonium, in addition to the calyptra, but only in *Calycularia* is there an involucre in addition to a perianth. Except in *Pellia* and *Calycularia*, there is a definite differentiation of the plant-body into stem and leaves.

The simplest type of vegetative structure is found in *Pellia*, in which the thick median portion of the thallus passes rather gradually into the thinner lateral wings. In *P. epiphylla* many of the cells have broad ribbon-like thickenings on the walls; usually each cell has only a single band, and in a longitudinal section of the thallus the bands are seen to be arranged in lines running from the upper to the lower side. These bands are also found in the thallus of *P. Neesiana*, but are absent from *P. calycina*; both these species differ from *P. epiphylla* in being diœcious. Though *Pellia* is so largely studied as a type in elementary teaching, the descriptions given in text-books are mostly very inaccurate in various points; this is partly due to the fact that the three species just mentioned—the only species of the genus, and all occurring in Britain—are frequently confused with each other. The antheridia are sunk separately in cavities, scattered over the upper side of the thick median region of thallus. The archegonia are developed in groups,

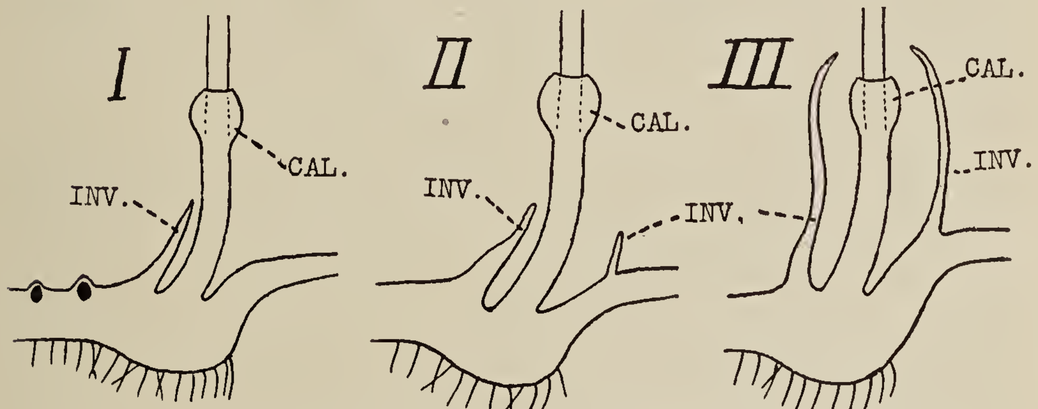


Fig. 39. Diagrammatic longitudinal sections through the calyptra and involucre of (I) *Pellia epiphylla*, (II) *P. Neesiana*, (III) *P. calycina*.

each group becoming sunk in a pocket-like cavity which opens in front, the archegonia being directed horizontally and accompanied by short mucilage-hairs. The margin of this pocket shows differences characteristic of the three species. In *P. epiphylla* and *P. Neesiana* it forms a short involucre beyond which the calyptra of the ripe sporogonium extends for some distance, whilst in *P. calycina* it forms a long bell-like envelope enclosing the calyptra. In *P. epiphylla* the involucre or pocket-margin grows out only on the posterior side, forming a hood-like scale, but in *P. Neesiana* it grows out all round as a short collar-like sheath (Fig. 39).

In the young capsules of *Pellia*, after the capsule-wall has become differentiated as an outer layer of large cells and (usually) two inner layers of small cells, but before one can distinguish between the spore-mother-cell and those which will later form the free elaters mingled with the spores, the inner tissue (endothecium) shows a fairly sharp separation into two portions—a sterile basal portion extending from the bottom of the capsule and spreading out fanwise as seen in longitudinal section, and a fertile portion which extends over the top of the columella-like basal tissue. The columella, or elaterophore, consists of elongated cells, forming a bundle of fixed elaters. In *P. calycina* (23, 36) the fixed elaters of this bundle (about a hundred in number) are much longer than the free elaters and often reach more than half-way up the capsule; like the free elaters which are mingled with the spores, they usually have a double spiral band. In *P. epiphylla* the fixed elaters are fewer in number (thirty to fifty), shorter, thicker, and furnished with from one to four spiral bands. *P. Neesiana* resembles *P. epiphylla* in the structure of the capsule; in these two species the inner layers of the capsule wall bear ring-like fibres, which are lacking in *P. calycina*. When the capsule opens the four valves move outwards and downwards, exposing the mass of spores and loose elaters, which are held together for a time by the tuft of fixed elaters, the mass then becoming loosened by the hygroscopic movements of the elaters and gradually shaken out.

The basal tuft of fixed elaters in the capsule of *Pellia* arises in the same way as the apical sterile tissue forming the elaterophore of *Aneura* and *Metzgeria*. The differences in the mature structure of the columella and in its behaviour when the capsule dehisces, are clearly connected with the difference in position. In *Aneura* the apical columella remains coherent until the capsule dehisces, when it splits into four portions, one of which remains attached to the tip of one of the valves of the capsule-wall; whilst the basal columella of *Pellia* splits up into long elater-like cells and forms a mop-like tuft which holds the spores and free elaters loosely together, and assists in their general dispersal.

In *Calycularia*—a genus which, as Schiffner has pointed out, (57, 58), has generally been confused with *Mörckia*—the thallus resembles that of *Pellia* in form, but there is a sharper distinction between midrib and wings, and on the lower side of the midrib there are developed, chiefly at the growing point, small leaves comparable with the ventral scales of the Marchantiales or the amphigastria of the Acrogynæ. The archegonial group is protected by a series of scales, and, after fertilisation, there arises within these a bell-like perianth, as in *Mörckia*. The capsule, however, strongly resembles that of *Pellia* in structure; the wall consists of two layers of cells bearing fibrous thickenings, and at the base of the cavity there is a tuft of fixed elaters, exactly as in *Pellia*; the ripe capsule opens by a varying number of valves.

Noteroclada (*Androcryphia*)[1] is also closely allied to *Pellia*, but here the plant-body is differentiated into stem and leaves, the latter being nearly semi-circular and inserted by a broad base on the cylindrical stem. The growing-point has a three-sided apical cell; each lateral segment gives rise to a leaf, whose insertion is at first transverse to the long axis of the stem, but later becomes shifted so as to be horizontal, and eventually the anterior edge of the leaf lies below the posterior edge of the leaf in front (succubous leaf-arrangement); from each ventral segment there grow out four mucilage-hairs, representing a ventral scale or amphigastrium. The leaves are one cell thick, except at the base, where there are several layers of cells. Apart from the different form of the apical cell and the different organisation of the vegetative organs, *Noteroclada* is clearly related to *Pellia*; each antheridium is sunk in a cavity of its own, and the capsule agrees very closely with that of *Pellia*—there is a basal tuft-like elaterophore, and the spores begin to germinate and become multicellular before the dehiscence of the capsule, which takes place by four valves. This premature germination of the spores, however, occurs in several unrelated Hepatics, e.g. *Fegatella* and *Dendroceros*. In *Noteroclada* the archegonia are not sunk in a cavity, as in *Pellia*, but arise from the upper surface of the stem and are protected by the young leaves at the stem-apex; but this difference is clearly correlated with the fact that *Pellia* is thalloid while *Noteroclada* is foliose. Stephani (66) says that *Noteroclada* is so near *Pellia* that it should perhaps be included in that genus, and that it is practically a *Pellia calycina* with stem and leaves instead of simple thalloid plant-body.

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[1] Professor Goebel, in a recent letter to the writer, announces that he has been fortunate enough to obtain living material of this interesting and rare type, and that its structure and development are under investigation at Munich.

In *Blasia* there is a broad stem bearing on either side a row of large leaves lying in the same plane as the broad midrib or stem, and not so sharply separated from it as in *Noteroclada*. In addition to the leaves, *Blasia* developes an extraordinary diversity of appendages—*Nostoc*-auricles and amphigastria on the lower surface, curious flask-like gemma-receptacles and star-like gemmæ on the upper surface. The amphigastria on the lower side and the star-like gemmæ (5) on the upper are alike in structure, being cell-plates attached by a short stalk at the centre; the former stand singly at the junction of leaf and stem, the latter are scattered over the upper side of the thallus and on being detached give rise to new plants. The long-necked gemma-flasks have been described and figured already in this journal (7). The *Nostoc*-appendages (17, 41, 53, 70), of which there are usually two to each leaf, when ready for infection by *Nostoc*, are rounded pockets, each formed from a cell which projects from the thallus and divides transversely, cutting off a terminal club-shaped slime-secreting cell, around which the auricle grows like a hood by division of the underlying cell. After the entrance of the *Nostoc*, the opening closes up and the whole auricle increases in size; as the *Nostoc* chains grow, the slime-secreting cell projects into the cavity and branches to form a tree-like structure, the ramifications of which doubtless absorb nourishment from the algal cells. The flask-like gemma-receptacles are probably modified archegonial receptacles, since archegonia are sometimes found in these flasks. The antheridia and archegonia have the same arrangement and structure as in *Pellia*, but the capsule (1, 52) differs considerably from that of *Pellia*, being elongated and having its basal portion produced downwards as a collar around the top of the seta. There are no ring-like fibres in the capsule wall, which consists of an outer layer of large cells with rodlike thickenings on the radial walls, and two or three inner layers of flattened and thin-walled cells; at the base of the capsule there are a few fixed elaters, representing a rudimentary elaterophore.

The Japanese genus *Cavicularia* closely resembles *Blasia* in vegetative structure, having similar leaves, *Nostoc*-appendages, amphigastria, and antheridia, but its sporogonia have not been discovered. Two kinds of gemmæ are produced, according to Schiffner (56); some are lens-shaped, others spherical, and both kinds are produced in crescent-like receptacles resembling those of *Lunularia.* The archegonia are developed in receptacles exactly like those containing the gemmæ, the latter being produced on the sterile female plants; sometimes, in fact, the archegonia occur in groups in the gemma-receptacles themselves. It seems probable that in both *Blasia* and *Cavicularia* we have an example of the replacement of spore-production by asexual propagation; *Blasia* is more often found with gemma flasks than with fruits, and apparently in *Cavicularia* fruits are very rarely formed and have not yet been discovered.

In *Fossombronia*, which is the largest genus of Codoniaceæ, having nearly fifty species, the plant has the same general habit as that of *Noteroclada*, but the stem is broader, and sometimes the leaves are no more sharply marked off from it than in the case of *Blasia.* There are small ventral scales near the growing point (33), serving for the protection of the latter and soon perishing; the underside of the stem bears numerous rhizoids, which usually have a characteristic deep reddish-violet colour. In some species, e.g., *F. longiseta*—recently described in detail by Humphrey (35)—the stem is thickened to form a tuber in which food is stored; while in *F. tuberifera*—discovered by Goebel (17)—the plant periodically grows down into the soil, the leaves becoming greatly reduced in size and the end of the stem swelling to form a tuber which passes through a resting stage and afterwards resuming growth to form an ordinary leafy shoot. The antheridia are scattered singly over the stem, close to the leaf-bases, and are sometimes protected by a scale growing from the stem tissue immediately behind the antheridium. The archegonia are developed in small groups, on the middle or sides of the stem; after fertilisation an envelope (perianth) arises, as in *Noteroclada*, as a ring-like outgrowth from the stem tissue surrounding the group. The capsule-wall has an outer layer of unthickened cells and an inner layer of cells bearing thick half-ring fibres, often very irregularly arranged. The elaters are short and there are usually no fixed elaters, or very few, at the base of the capsule. Sometimes the ripe capsule dehisces by four valves, but more often the upper portion of the wall breaks up into irregular plates which are thrown off, leaving the mass of spores and elaters held in the saucer-like lower portion of the wall.

The curious genus *Petalophyllum* (8, 48, 69) is closely allied to *Fossombronia*, but in vegetative structure it strongly resembles *Geothallus*. The plant is fan-shaped, expanding from a narrow cylindrical basal portion. On either side of the stem there is a horizontal wing bearing vertical laminæ, which run forwards and outwards (Figs. 40, 41). The lamellæ are one cell thick and are often arranged with great regularity in two series, one on either

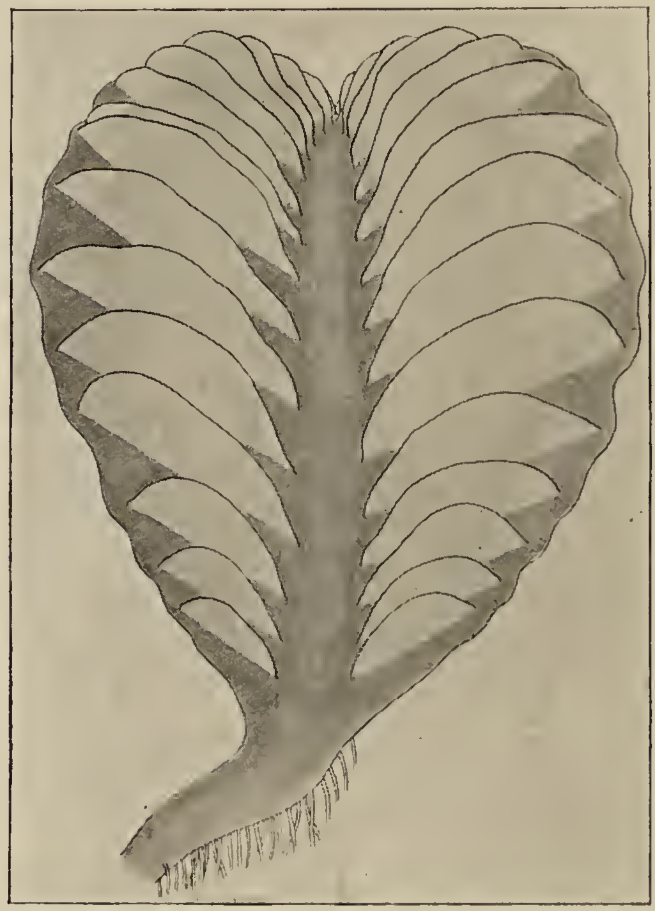


Fig. 40. *Petalophyllum ralfsii.* Plant as seen from above. ×8.

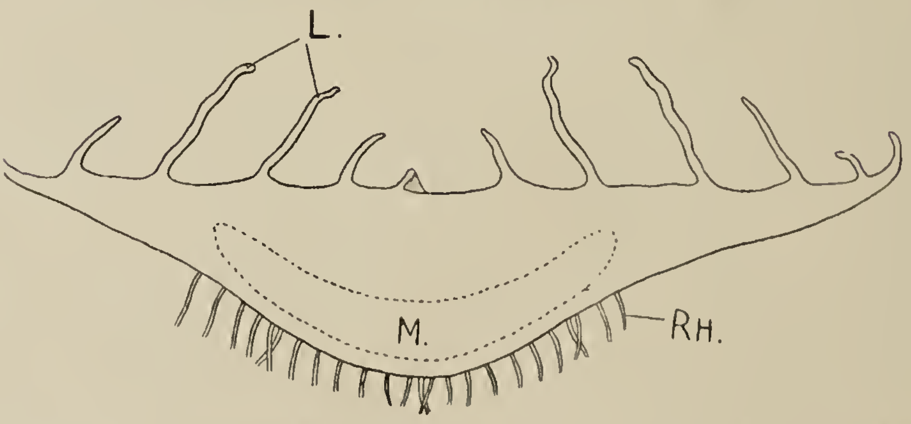


Fig. 41. *Petalophyllum ralfsii.* Transverse section through the middle of the leaf-bearing region of the plant. *L.*, leaves; *M.*, mycorhiza; *Rh.*, rhizoids, ×20.

side of the middle line. The plant grows near the sea, and periodically becomes buried in the sand, forming a tuber in which food is stored (Fig. 43). The leafy portion of the plant dies down,

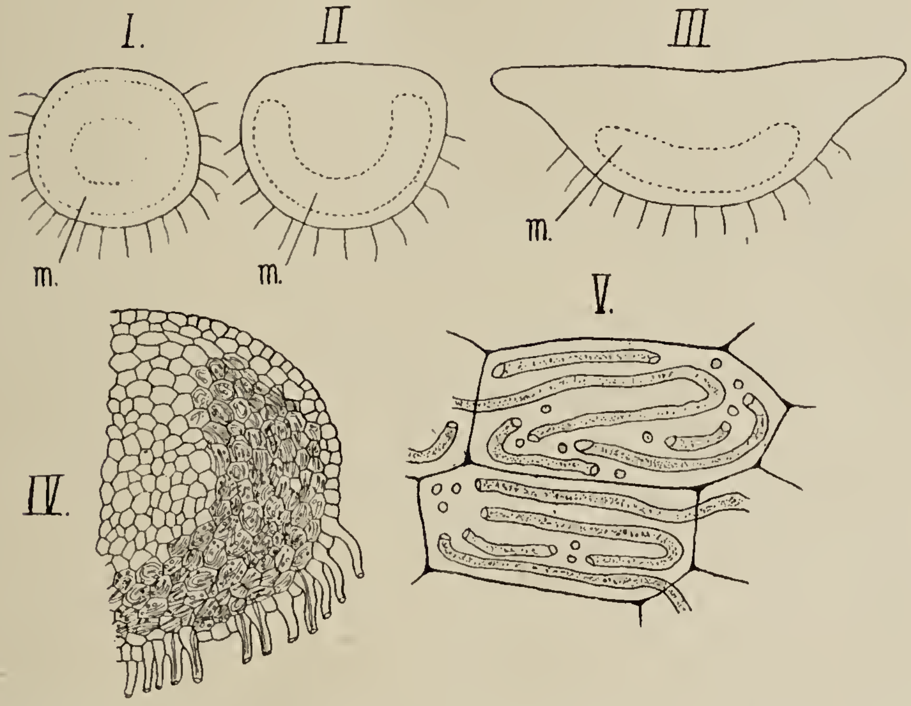


Fig. 42. *Petalophyllum ralfsii.* I-III, Successive transverse sections of the stem, ×20; *m*, mycorhizal zone. IV, Part of I, ×50, showing fungal hyphæ traversing the rhizoids and ramifying in cells of mycorhizal zone. V, Two cells containing hyphæ, ×350.

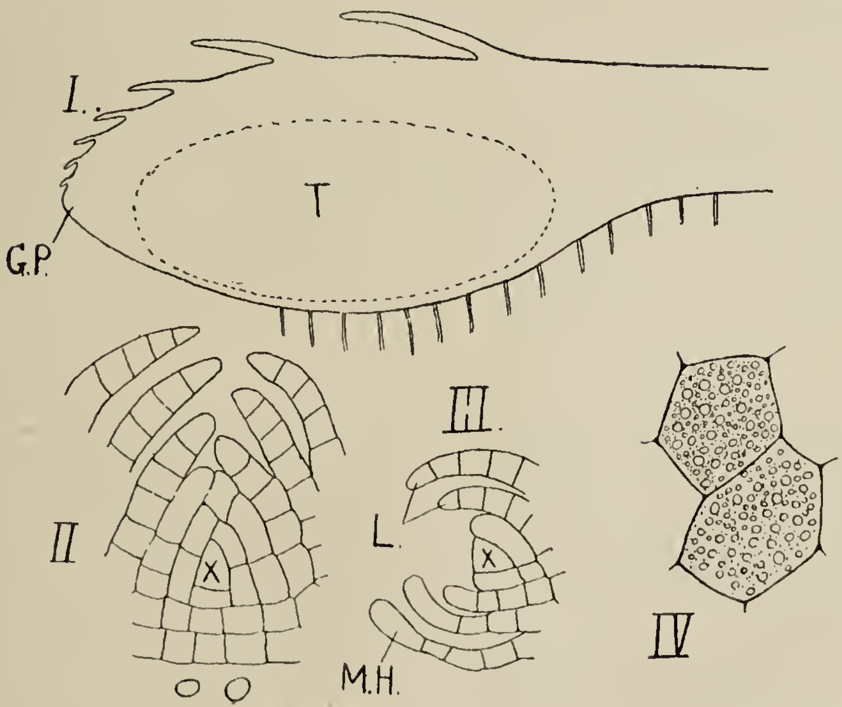


Fig. 43. *Petalophyllum ralfsii.* I Longitudinal section through apex of of stem, showing the tuberous swelling (T) behind and below the growing-point (G.P.). II, Transverse section of growing-point, showing the apical cell (X). On either side are the young leaves (L.); below are two mucilage-hairs in cross-section. III, Part of a longitudinal section through the growing-point. *L.*, leaves; *M.H.*, mucilage-hairs. IV, Two cells in the tuber, showing densely granular contents. I, ×20; II, III, ×150; IV, ×350.

and when growth is resumed the first-formed portion of the new shoot consists of stem only, but later the leaves appear and the stem expands laterally to form the broad wing which carries the leaves (laminæ) on its upper side. The antheridia are developed in a group behind the apex and are protected by small scales. The archegonial group becomes surrounded by an envelope formed in the same way as in *Fossombronia*, and in the structure and dehiscence of the capsule *Petalophyllum* closely resembles that genus.

Treubia insignis, a very beautiful plant discovered by Goebel in Java (20) and later in New Zealand (26), is the largest of the dorsiventral leafy Anacrogynæ, and shows the mostly highly diffentiated leaves. The apical cell is three-sided, as in *Noteroclada* and *Petalophyllum*, and the leaves, at first inserted transversely on the stem, eventually become oblique, the insertion of each leaf sloping downwards and forwards (succubous). At the front of each leaf, on its upper side, there is a small lobe or scale which projects inwards over the upper surface of the stem and forwards beyond the insertion of the leaf (Goebel's "Organography," Figs. 165 and 166). The antheridia and archegonia are developed on the sides of the stem and are protected by the scales of the leaves. There is no perianth, but the developing sporogonium is protected by a thick calyptra, which, as in *Aneura*, is formed from the stem tissue around the archegonial group. The spherical capsule dehisces by four valves; the wall consists of three or four layers of cells, the outer cells being large and flattened and devoid of thickenings, while those of the inner layers have numerous half-ring fibres, or, in some cases, a spiral fibre; at the base of the capsule there are a few fixed elater-like elongated cells, representing a rudimentary elaterophore.

CALOBRYACEÆ.

This family, consisting of the two genera *Haplomitrium* and *Calobryum* is one of the most remarkable and interesting among the Bryophyta. The former genus has a single species (*H. Hookeri*) apparently confined to Europe (27, 34, 46, 52); *Calobryum* has three species, found in Java and New Guinea, in Japan, and in South America respectively (17, 21, 54, 66).

The Calobryaceæ differ considerably in vegetative structure from all other Hepaticæ. The plant consists of a branching underground rhizome-like portion, without rhizoids; from this leafless rhizome there spring erect leafy shoots, each growing by a three-sided apical cell and consisting of a cylindrical stem and spirally arranged leaves. Müller (52) in his description of *Haplomitrium*, states that the leaves are irregularly disposed on the stem, but Stephani (66) states that in both genera there is a distinction between two rows of obliquely inserted leaves, and a third row of transversely inserted leaves, the latter corresponding to the ventral leaves or amphigastria of the Acrogynæ. Goebel (21) describes the same arrangement in *Calobryum Blumei*, where the transversely inserted row, consists of leaves only half as large as those in the other two rows.

In *Haplomitrium* the shortly-stalked ovoid antheridia are borne, usually in groups of two or three, in the axils of the upper leaves of the male plant; according to Stephani they are never found in the axils of the transversely inserted leaves (amphigastria), but Müller (52) says that they are arranged all round the stem and may also occur on the stem surface without any relation to the leaves. Gottsche in his classical memoir (27) gives the same account as Müller. The archegonia are also developed in the axils of the uppermost leaves of the female plant, these leaves being usually larger than the others; there is no involucre or perianth, but the sporogonium is protected by a large cylindrical calyptra. The development of archegonia does not arrest the apical growth of the shoot; the apical cell is not used up in the formation of an archegonium, and sometimes the apical growth of the shoot is resumed after the formation of a sporogonium. The oblong capsule usually opens by two or three valves; the wall consists of a single layer of cubical cells, each having a single thickened ring-like band extending over the horizontal and tangential walls of the cell, instead of being set transversely to the long axis of the capsule as are the ring fibres in the capsule-wall of other Hepaticæ.

In *Calobryum*, which has the same general habit as *Haplomitrium*, the leaves are apparently arranged more definitely in three rows, and both the antheridia and the archegonia are developed in groups on the flattened and broadened apex of the stem. In both cases the group of sexual organs is surrounded by three large spreading leaves, so that the plant has a close superficial resemblance to the male "flower" of *Funaria* or *Mnium*. In the development of the archegonia, the apical growth of the plant is arrested, hence *Calobryum* is definitely acrogynous. The sexual organs, calyptra, and sporogonium have the same structure as in *Haplomitrium*.

INTER-RELATIONSHIPS OF THE ANACROGYNÆ.

With the exception of the Calobryaceæ, the four families into which we have here divided the Anacrogynæ are somewhat artificial. The classification and phylogeny of the Anacrogynæ present great difficulties. It might be expected that the great diversity in both gametophyte and sporophyte shown by the genera of Anacrogynæ would make it comparatively easy to arrange them in a natural classification, but it is just this diversity, together with the frequent occurrence of parallel developments in different lines, that baffles our attempts to frame a satisfactory arrangement. For instance, the genera *Aneura* and *Pellia* present the simplest type of gametophyte along with the most advanced type of sporogonium, if one may assume that the undifferentiated thallus is really the primitive type of plant-body and that the sporogonium which shows the earliest and most extensive sterilisation of "potentially sporogenous tissue" is the highest type of sporophyte. Both of these assumptions have been challenged, the former by Wettstein and the latter by Goebel and others, but the questions raised will be considered later when discussing the general phylogeny of the Bryophyta.

Various writers have attempted to draw sharp distinctions between "thallus-lobes" and "true leaves" in the Anacrogynæ, but these supposed distinctions are based upon somewhat narrow morphological ideas derived from the study of the Acrogynæ. For instance, Stephani (66) describes *Blasia*, and even *Treubia* (62) as having a "lobed thallus," though he applies the term "leaves" to the appendages of the axis in *Fossombronia* and *Noteroclada*. Yet in all four genera the appendages arise in essentially the same way at the growing-point, an appendage being formed from each lateral segment cut from the apical cell and having therefore a definite position with reference to the axis.

In the Anacrogynæ the growth of the plant-body is always referable to a single apical cell, the form and mode of segmentation of which show great diversity in the various genera and even differ in different species of the same genus. Still, the mode of apical growth is of interest and even of value, in helping us to understand the morphology of the plant-body, with special reference to the origin of the differentiation into stem and leaves of the presumably primitive thallus—a differentiation which has clearly arisen in several distinct lines and by several distinct methods.

The simplest type is, apparently, the "two-sided" apical cell, that is, a cell from which two sets of lateral segments are cut off, alternately right and left. An apical cell of this kind occurs in *Aneura*, *Metzgeria*, *Podomitrium*, *Umbraculum*, *Symphyogyna*, and *Fossombronia*. In each case the apical cell is triangular as seen in a surface view of the growing-point (or a horizontal section through it) and only two sets of segments are cut from it, but there are differences in detail as regards the relation of the apical cell to the tissue formed by the further divisions of the segments. In *Metzgeria*, for instance, the apical cell is nearly square as seen from the front, and nearly hemispherical as seen in a vertical longitudinal section through the growing-point. In the other genera, however, a smaller portion of the apical cell is exposed on the upper and lower sides, the dorsal and ventral tissue covering it to a varying extent. This is due to the more active growth of the upper and lower portions of each lateral segment, the midrib in these genera being more massive than in *Metzgeria*. In *Fossombronia*, this rapid growth of the segments is especially marked, and the apical cell has the form of a spindle, elongated vertically, when seen from the front. In *Metzgeria*, *Podomitrium*, *Umbraculum*, and *Symphyogyna*, each segment divides first by a vertical wall into an inner (adaxial) and an outer (abaxial) cell; the latter divides only by walls vertical to the plane of the thallus and forms the single-layered wing, while the former divides also by walls parallel with the surface of the thallus and contributes to the formation of the midrib. In the wingless species of *Aneura*, all the cells formed from the segments divide by both horizontal and vertical walls, so that the thallus is several layers in thickness. In *Fossombronia*, each lateral segment divides first by two superposed horizontal walls; the upper and lower cells contribute to the formation of the stem, while the middle cell grows out to form a leaf.

In *Blyttia*, *Mörckia*, *Blasia*, and *Pellia calycina*, the apical cell is wedge-shaped, four sets of segments being cut from it—dorsal and ventral segments as well as right and left lateral segments. In a vertical longitudinal section through the growing-point, the apical cell is triangular, while in surface view or horizontal section it is usually four-sided. The dorsal and ventral segments contribute to the thick axial portion of the plant-body. In *Blyttia* the lateral segments divide in much the same way as in *Metzgeria*; in *Pellia calycina* their division resembles what is seen in the wingless species of *Aneura*; and in *Mörckia* we have a transition between the two types, the thick median portion of the thallus usually thinning out into the wing on either side more abruptly than in *Pellia calycina.* In *Blasia*, the lateral segments divide in practically the same way as in *Fossombronia*, horizontal divisions giving three superposed cells of which the dorsal and ventral add to the stem tissue while the middle cell forms a leaf.

In *Pellia epiphylla* the apical cell is semi-circular in a vertical longitudinal section through the growing-point, and there are cut from it three sets of segments, two lateral and one posterior, the latter extending the whole depth of the thallus and only later dividing into dorsal and ventral cells. As Campbell (6) has pointed out, this type has probably been derived from the wedge-shaped type (with four sets of segments) "by a gradual increase in the angle formed by the dorsal and ventral walls of the apical cell, which finally became so great as to form practically one plane." The midrib is usually decidedly thicker, vertically, in *Pellia calycina* than in *P. epiphylla*, and the differences in the form of the apical cell and its mode of segmentation may perhaps be connected with this difference in the depth of the midrib in the two species.

Finally, in *Noteroclada*, *Petalophyllum*, *Treubia*, and the Calobryaceæ, we have a tetrahedral cell, similar to that found in most of the Acrogynæ and Mosses, from which three sets of segments are cut off in spiral succession. In the Calobryaceæ, which grow erect and are more or less distinctly radial in symmetry, each segment produces a leaf, but the leaves of one row are frequently, if not always, either larger or smaller than those of the other two rows and further differ from them in being inserted transversely instead of obliquely on the stem, so that even in this group we get the bilateral symmetry and anisophylly which are so characteristic of the Acrogynæ. In the other three genera of Anacrogynæ with a tetrahedral apical cell, the plant grows horizontally and is bilaterally symmetrical, and leaves are only formed from the lateral (strictly, dorso-lateral) segments, though in *Noteroclada* and *Petalophyllum* each ventral segment produces hairs which represent the ventral leaves or "amphigastria" of the typical Acrogynæ. In *Noteroclada*, the upper portion of each dorso-lateral segment contributes to the formation of the stem, while the lower portion grows out to form a leaf; in *Petalophyllum*, each dorso-lateral segment divides, like the lateral segments in *Fossombronia*, into three superposed cells, of which the dorsal contributes to the midrib and the ventral to the wing on either side of the midrib, while the middle cell forms one of the lamellæ on the upper surface of the wing.

The differentiation of the plant-body into stem and leaves is associated with all the three chief types of apical cell found in the group—the "two-sided" *Metzgeria* type, the "four-sided" or wedge-shaped type, and the tetrahedral type. This fact strengthens the evidence, drawn from other considerations, that leaves have evolved independently in several distinct lines of relationship among the Anacrogynæ. Whatever the form of the apical cell, each lateral segment divides at an early stage into a portion which contributes to the thicker axial region of the plant-body and a portion which grows out and gives rise either to a continuous wing or to a leaf. Absolutely no morphological distinction can be drawn between a plant-body with a midrib and lobed wings, as seen in species of *Symphyogyna*, and one with distinct stem and leaves. We find in the Anacrogynæ every stage in the transition from a thallus with a continuous entire wing to a sharply differentiated leafy shoot, and the differences which are seen in the mature plant-body are differences of degree only. For instance, in *Blasia* the inner or axis-forming portion of each lateral segment grows more actively than is the case in *Fossombronia*, hence in the former genus the stem is broader and the leaves less sharply marked off from it than in the latter. The same explanation may be applied to those species of *Blyttia* and *Symphyogyna* in which the wing is either regularly and deeply lobed or bears regularly arranged filamentous marginal appendages. If the outer portions of the lateral segments grow uniformly, those of successive segments remaining coherent, we get a thallus with or without sharp distinction into midrib and wings; if the outer portion of each segment grows out independently, we get a leafy stem; and between the two extremes we get all stages of transition.

The only Anacrogynæ in which the plant-body is purely thalloid and shows no signs of differentiation into stem and leaf are *Pellia*, *Calycularia*, *Makinoa*, *Mörckia*, and the four genera we have classed under Aneuraceæ. In all these genera there is a more or less marked midrib with a thin wing on either side, though in some species of *Aneura* this differentiation is not shown.

In *Umbraculum* and the "Dendroid" species of *Blyttia* and

Symphyogyna, however, the plant-body is differentiated into a creeping wingless sympodial rhizome and an erect fan-like assimilating portion formed by repeated "dichotomy" of a winged axis. In these three genera, as well as in *Podomitrium*, the axis is traversed by a strand of pitted cells; in *Podomitrium* and in the creeping species of *Blyttia* and *Symphyogyna*, the strand is less strongly developed than in *Umbraculum* and the "Dendroid" species of *Blyttia* and *Symphyogyna*; in the "Dendroid" forms, again, the strand is more bulky in the erect than in the creeping portion of the plant. The observations of Tansley and Chick on *Mörckia hibernica* and *M. Flotowiana* (syn. *M. hibernica*, var. *Wilsoniana*) have already been referred to. In the latter species the writer found (9) that in the new branches produced by plants cultivated in glass-covered dishes in moist conditions (the plants came from sandy flats on the Yorkshire coast), the midrib showed no trace whatever of the two conducting strands which are normally present. It may be noted that several species of *Aneura* show a close approach to the "Dendroid" habit found in the genera *Blyttia*, *Symphyogyna*, and *Umbraculum*, though in *Aneura* the assimilating portion shows pinnate instead of fan-like "dichotomous" branching.

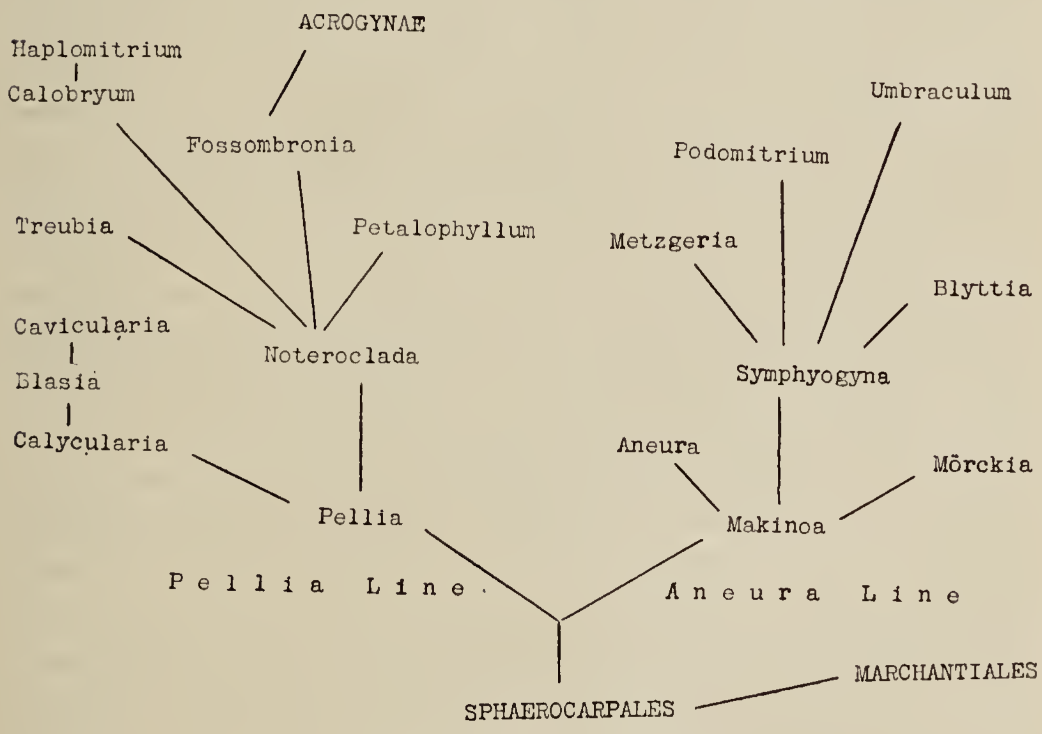
It is clear that both the "Dendroid" habit and the conducting strands have arisen independently in the different genera in which these developments occur. The most striking form of parallelism met with in the Anacrogynæ, however, is that which has led to the differentiation of the plant-body into stem and leaf. This is seen in its simplest form in those species of *Blyttia* and *Symphyogyna* in which the wing of the creeping thallus bears on its margin regularly arranged filamentous outgrowths or teeth, one such outgrowth being formed from each lateral segment of the apical cell. As Goebel (24, 26) has suggested, the primary function of these outgrowths is the protection of the growing-point, and it would seem reasonable to extend this view to account for the evolution of leaves in general. Where no leaf-like outgrowths arise from the lateral segments of the apical cell, the growing-point is provided with gum-secreting papillæ which arise from the cells above or below the apical cell, or from the segments at either side of it, or in all these positions. In many cases, the leaves arise in exactly the same way, the young leaf forming at first a unicellular club-shaped gum-papilla, which by active growth and divisions in the cell that bears it, becomes terminal on a cell-row or a cell-plate. Apart from *Blyttia* and *Symphyogyna*, in which the evolution of leaves only occurs in certain species, and the leaves themselves are in these species inconspicuous (except at the growing-point) owing to their early loss of individuality, of the eighteen Anacrogynous genera here dealt with, no less than eight are distinctly foliose. The vegetative organisation of these genera (*Noteroclada*, *Blasia*, *Cavicularia*, *Fossombronia*, *Petalophyllum*, *Treubia*, *Haplomitrium*, and *Calobryum*) has already been described in some detail.

The Calobryaceæ stand well apart from the other Anacrogynæ, but the three remaining families are connected by cross-affinities, besides showing parallel developments in the position, investment, and structure of the sexual organs and sporogonia, as well as in the vegetative organs. The Aneuraceæ and Blyttiaceæ have elongated capsules (except *Metzgeria*), with a more or less highly developed apical elaterophore. Only in *Aneura* and *Metzgeria* is this structure an efficient mechanism for active spore-dispersal, for in these genera alone does the capsule-wall regularly split into four valves, each bearing at its tip a quarter of the split-up elaterophore; in the other genera the capsule dehisces by a varying number of valves which usually remain coherent at the tip. In all the genera placed in these two orders, with the exception of *Aneura* and *Metzgeria*, the fibrous thickenings in the capsule-wall are either absent or feebly developed, while the elaterophore is represented by a flattened cap of cells with some elater-like outgrowths hanging down into the cavity of the capsule. Apart from the restriction of the sexual organs to special short branches (lateral in *Aneura*, ventral in the other three genera) there is no constant character separating the Aneuraceæ from the Blyttiaceæ. As regards the investment of the sporogonium, two genera in each family have no well-developed envelopes outside the calyptra, which is massive and fleshy (*Aneura*, *Metzgeria*, *Symphyogyna*, *Makinoa*). A tubular envelope ("perianth") is present in *Podomitrium*. *Umbraculum*, *Blyttia*, and *Mörckia*, surrounding the archegonial group and arising either before or after fertilisation of one of the archegonia; in these four genera there is an additional investment ("involucre") outside the perianth, consisting of a single scale (*Umbraculum*) or of a cupule-like circle of scales. In *Symphyogyna* and *Makinoa*, there is also a single involucral scale, as in *Umbraculum*; in *Aneura* and *Metzgeria*, the archegonia are protected by the incurved edges of the short female branch, and the young sporogonium by the thick calyptra. Little can be inferred from these different arrangements, beyond the generalisation that while a short collar-like outgrowth, or a circle of scales, or a single scale, or the inturned and fringed edges of the female branch, suffices for the protection of the archegonia (by forming capillary water-holding spaces), the developing sporogonium requires a more complete cylindrical investment which may be provided in the form of a massive calyptra or of a special tubular outgrowth of the surrounding tissue.

The thick calyptra on the one hand, and the tubular perianth on the other, have apparently arisen independently in several lines of development; we meet with both in genera belonging to the other groups—the perianth in *Calycularia*, *Noteroclada*, *Fossombronia*, and *Petalophyllum*, and the massive calyptra in *Treubia* and the Calobryaceæ. In all the foliose Codoniaceæ (except *Blasia*), as in the Calobryaceæ, the archegonia are protected by the leaves; in *Blasia* and in *Pellia* they are sunk in a cavity in the axis of the plant-body, and in *Calycularia* there is a cupule-like involucre formed from scales. In all the Codoniaceæ, except *Blasia*, the capsule is spherical, and its wall is provided with fibrous thickenings. In *Fossombronia* and *Petalophyllum*, the capsule-wall breaks up into plates, and there is no trace of an elaterophore, but in the other genera, dehiscence occurs by four valves and there is always a more or less highly developed basal elaterophore. The latter reaches its greatest development in *Pellia* and *Noteroclada*, but in most of the other genera is represented only by isolated fixed elater-like cells at the base of the capsule-cavity.

The Codoniaceæ are sharply marked off from the Blyttiaceæ and Aneuraceæ by the capsule structure, especially by the basal elaterophore. The two latter families should perhaps be merged into one. *Podomitrium* connects the Aneuraceæ with the Blyttiaceæ, having the following characters in common with the genus *Blyttia*: perianth laid down before fertilisation occurs in the archegonial group, and formed by outgrowth of several fringed scales which are carried up to form a tube by basal growth; cells of capsule-wall uniformly thickened, without fibres; elaterophore represented only by an apical pad of thin-walled cells; capsule-wall and elaterophore do not split at the top. In *Umbraculum*, which is frequently joined to *Podomitrium* to form the genus *Hymenophytum*, the perianth is laid down before fertilisation, and arises not from scales but from a ring-like outgrowth; the outer cells of the capsule-wall have fibrous thickenings; the capsule opens by four free valves, the elaterophore splitting into four parts which adhere to the tips of the valves, as in *Aneura* and *Metzgeria*. *Makinoa*, though probably more closely allied to *Symphyogyna* than to any other genus, resembles *Aneura* in having the antheridia sunk in chambers separated from each other by partitions two cells in thickness, each chamber opening by a pore on the upper surface of the thallus—but the antheridia are not developed on special short branches as they are in *Aneura*. Again, *Calycularia* shows some resemblances to *Mörckia* and *Blyttia*, e.g., in having a cupule-like scaly involucre in addition to a perianth, but in the structure of the sporogonium it agrees closely with the Codoniaceæ.

Although many of these resemblances are doubtless due to the occurrence of parallel developments, we may perhaps regard the Anacrogynæ as having diverged along two lines, which we may call the "*Aneura* line" and the "*Pellia* line," though these two genera have highly specialised sporogonia and are somewhat isolated from the genera with which we have classified them. In the *Aneura* line, including the Aneuraceæ and Blyttiaceæ, the most characteristic feature is the sterilisation of the central apical portion of the sporogonial tissue to form an incomplete columella or elaterophore; while in the *Pellia* line there is a corresponding basal sterilisation to form an elaterophore which projects upwards into the cavity of the capsule. That the elaterophore reaches its highest development in the genera *Aneura* and *Pellia*, while the vegetative structure of



Phylogeny of the Anacrogynæ.

the plant-body is simpler in these genera than in the other Anacrogynæ, may perhaps be accounted for by the fact that *Pellia* and probably the majority of the species of *Aneura* are more hygrophilous than any of the other Anacrogynæ; the three species of *Pellia*, and the terrestrial species of *Aneura* (the winged species are mostly epiphytic), grow in very wet places, and are often submerged in part. The peculiar gemmæ of *Aneura* strongly recall the zoospores of the green Algæ; "the absence of cilia from these cells, which probably are the last reminiscences of the ciliated gonidia of the aquatic ancestral forms, is to be accounted for by the terrestrial habit of *Aneura*" (Campbell). In dealing with the genus *Monoclea*, it was suggested that the formation of a long seta, in which this genus differs from its allies among the Marchantiales, might be correlated with the extremely hygrophilous habitat. The same explanation may be applied to the presence of the highly developed elaterophore of *Aneura* and *Pellia*; in very moist habitats the possession of an efficient method of spore dispersal would probably be advantageous, and it may be noted that the seta is longer in *Pellia* than in any other Hepaticæ, while in *Aneura* the capsule-valves spring back suddenly and the spores are violently thrown out.

In both of these lines we get numerous parallel developments, especially in the vegetative structure of the plant-body and in the investment of the sporogonium. In *Aneura*, the sexual branches are simply ordinary branches which usually stop growing in length after producing the sexual organs, but frequently (especially in the case of male branches) they resume ordinary vegetative growth afterwards. It may be assumed that the ancestors of the *Aneura* line produced the sexual organs on the upper side of ordinary thallus-branches, and that the arrest of growth which normally occurs in *Aneura* when a branch has produced sexual organs is a later modification. The genus which, though showing sporogonial features peculiar to itself, comes nearest to realising such a type is *Makinoa*, which has a well developed elaterophore and an antheridial receptacle similar to that of *Aneura*, but developed on the ordinary thallus. *Mörckia* apparently belongs to the *Pellia* and *Makinoa* branch of the *Pellia* line, though its many-layered capsule-wall is peculiar. *Mörckia* stands higher than *Makinoa*, the *Aneura*-like massive calyptra of the latter being replaced functionally by a perianth, outside of which a scaly cupule (involucre) is developed; in *Makinoa* the involucre consists of a single scale. From a *Makinoa*-like form, the *Symphyogyna* branch of the *Aneura* line may be readily derived, by the differentiation of the thallus into a cylindrical midrib and single-layered wings. This *Symphyogyna* plexus has evidently given rise to *Blyttia*, *Podomitrium*, *Umbraculum*, and *Metzgeria*. Of these four genera, *Blyttia* differs from *Symphyogyna* in little except the development of a tubular perianth, but in the other three the sexual organs are restricted to ventral branches. *Metzgeria* shows the simplest type of sexual branches, but the most highly developed elaterophore; its midrib is slender and lacks the conducting strand present in the other genera of the plexus, and neither perianth nor involucre are developed. *Umbraculum* may be derived from a *Symphyogyna*-like form by the relegation of the sexual organs and the development of a perianth after fertilisation. In *Blyttia* and *Podomitrium*, which have many points of resemblance, the perianth is developed before fertilisation, and outside it there is a cup-like involucre; probably *Podomitrium* bears somewhat the same relation to *Blyttia* that *Umbraculum* does to *Symphyogyna*. A cup-like involucre and a perianth are also present in *Mörckia*, which further resembles *Blyttia*, *Podomitrium*, *Umbraculum*, and *Symphyogyna*, in having conducting strands, though these are feebly developed. But *Mörckia* does not appear to be closely related to the *Symphyogyna* series, and the same double investment of the sporogonium is found in *Calycularia*, which apparently belongs to the *Pellia* line. It is clear that the *Aneura* line is peculiarly rich in parallel developments, exhibited by the evolution of "Dendroid" thallus habit, of conducting strands, of leaves, of specialised sexual branches, and of sporogonial investments (involucre and perianth).

In the *Pellia* line, we may distinguish two diverging branches. One of these leads through *Pellia* and *Calycularia* to the foliose genera *Blasia* and *Cavicularia*. The other leads through *Pellia* to *Noteroclada* and the other typical foliose Codoniaceæ, and probably also to the Calobryaceæ and the Acrogynæ. *Treubia* is an isolated genus, with its peculiar vegetative structure and the investment of the sporogonium by a massive calyptra instead of a perianth. *Fossombronia* is closely allied to *Noteroclada*, but its sporogonium is very like that of *Petalophyllum*, though the vegetative organisation of the latter is peculiar. The Calobryaceæ make a distinct approach to the Acrogynæ, but they appear to form a blindly ending line of development, and it is more probable that the Acrogynæ have arisen from a type like *Noteroclada*.

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(To be continued).

ADVENTITIOUS BUDDING AND BRANCHING IN *CYCAS*,

By M. C. Stopes, D.Sc., Ph.D.

[7 Figures in the Text.]

WHILE I was in Japan (1907-1909) I had the opportunity of examining numerous specimens of *Cycas revoluta* living in the open, some of which were very old. Many of these were much branched in an irregular way. A photograph of some examples of the kind is given by Miyoshi[1] in his series of habit photographs of Japanese plants, and there are some drawings in Wieland's[2] work on the fossil cycads; while mention is made of branching Cycads by Caldwell[3], Pearson[4] and others.

The brief notices of the subject in the literature, however, had not prepared me for the frequency or the extent of the branched plants, which were often much more like bushes than like "palms." One specimen in particular was most noteworthy, and as it seems greatly to exceed, in the quantity of its branching, those hitherto mentioned. I give a small sketch of it (Fig. 8) which is traced from a photograph.

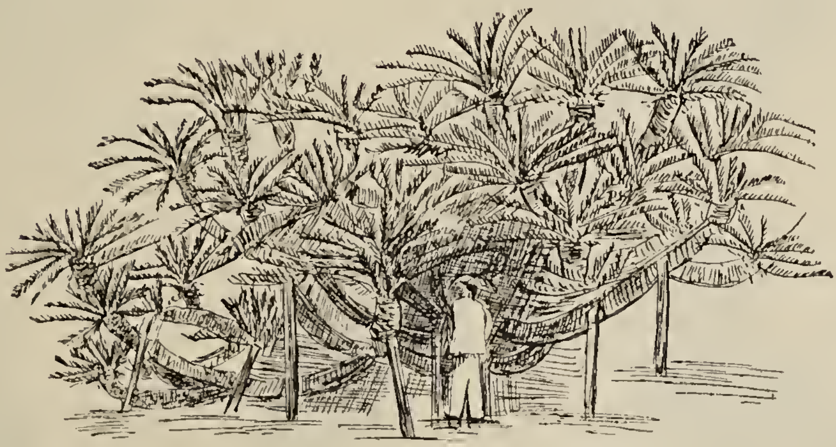

Fig. 8. A sketch of the much branched *Cycas* at Yejiri, traced from a photograph. The plant bore twenty-six huge male cones the year this photograph was taken, and had also innumerable crowns of leaves without cones.

The sketch does not show nearly all the detail of the plant, and gives but a poor idea of the enormous extent of the complex of branched trunks. The thick axes curve about in many directions and are propped up with strong supports, while the leaves of the leafy crowns interlock all over the surface. I counted twenty-six huge male cones on this plant on one of my visits to it. I had occasion to spend several days studying this and other plants in the neighbourhood and thus visited it more than once, though I was investigating another feature in it. I soon noticed the remarkable little bulbils which seemed to be growing all over the thick trunks. These varied much in size, and were to be found everywhere on the tree, even down to the very base of the oldest trunk. These buds, nearly full size, are seen in Fig. 9, (i), (ii), (iii) and (iv), in several of their early stages. Fig. 9 (iv) shows a complete isolated "bud," natural size, of the type commonest on the parent tree. The smaller buds, like that in Fig. 9 (i) *s* were also numerous, but largely hidden between the armoured scales of the corrugated leaf-bases.

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[1] Miyoshi, M. "Atlas of Japanese Vegetation," phot. 31.

[2] Wieland, G. R. "American Fossil Cycads," Carnegie Institute of Washington, 1906.

[3] Caldwell, O. W. "*Microcycas calocoma*," Bot. Gaz. 44, Aug., 1907.

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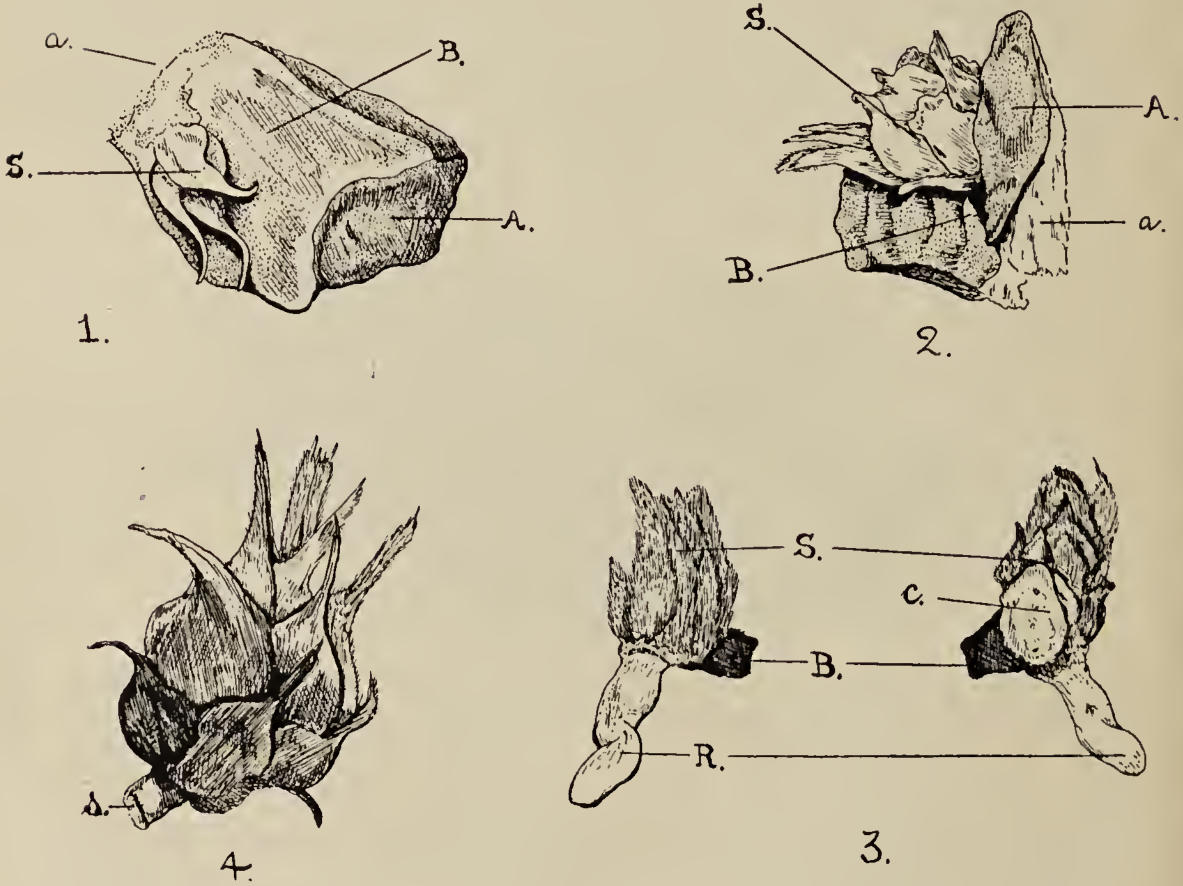

Fig. 9. A. Outer end of leaf base. B. Upper surface of leaf-base. *a*, end of leaf-base torn away from the stem-cortex.

(i.) Leaf-base detached, with a small "bud", *s*, growing on its upper surface.

(ii.) Older "bud" with hard outer scales and hairy inner ones seen between two leaf-bases.

(iii.) Two views of another "bud;" *s*, shoot with hairy scales, *c*, lateral attachment of the sprout to the leaf-base, R, root of sprout growing into the air.

(iv.) Older "bud" which has a short axial portion, *s*. This bud was in active growth, the inner hairy scales protecting small leaves.

As even the Tokio botanists to whom I mentioned my preliminary observations did not seem to have given the buds special attention, it appeared worth while to record the following facts about them.

The "buds" arise, apparently at any time and quite irregularly on the leaf-bases all over the older plants of *Cycas revoluta.* I counted back from the crown 228 whorls, and at this level found many of the small and flourishing buds growing on the leaf-bases all round the trunk.

Behind this region the whorls became indistinct and it was difficult to count accurately, but there must have been at least another 100 whorls, and even there the leaf-bases were fresh and bore "buds." Externally the old leaf-bases of *Cycas* appear to have entirely dried up and hardened, and they form, as is often described, a corrugated armour round the stem. As they were still capable of budding I cut into them and carefully examined their condition. The external blackened part is very hard and protected by several layers of cork; between it and the inner still fresh part of the leaf-base, are five or six areas cut off by successive active zones of cork. This is seen in Fig. 10.

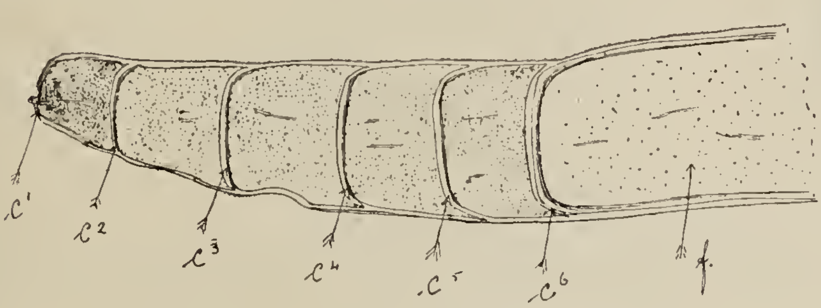

Fig. 10. Section through an old leaf-base showing successive zones of cork, c^1, c^2, etc., and the persistent base, *f*, packed with starch.

The zones between the cork layers contain much tannin, but the persistent base behind is fleshy and quite juicy and fresh. The cells in the latter region are packed with starch grains, and the vascular bundles and mucilage canals are all quite normal. It is from this fresh, basal portion that the "buds" spring.

The manner of their growth and the course of the vascular system in these buds is very various, but all the many I examined seemed (it was in some cases difficult to determine this absolutely) to arise from the leaf-base itself and *not* from the axis, or to be in any way connected with the axis at first. In some cases this is perfectly evident, as in Fig. 9 (i), where the "bud" lies on the surface of the leaf-base some distance from the axis. Without injuring the trees in a way that was not permissible it was not possible to collect all the material I should have liked; but I cut into the axis in several places and found leaf-bases still about an inch thick bearing buds which had no traces going back to the axis. In this connection an old wound on one of the trees should be mentioned. This wound had cut out an area of the leaf-bases about six inches square, leaving the axis itself exposed. No buds were formed in this region, though the leaf-bases round bore many, and some of these had exposed roots such as are shown in Fig. 9 (iii.) R and Fig. 11.

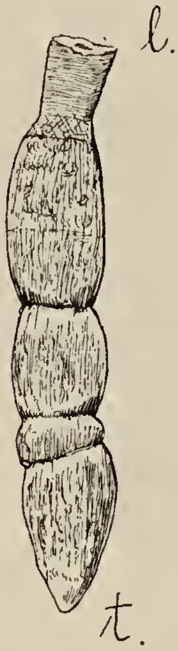

Fig. 11.

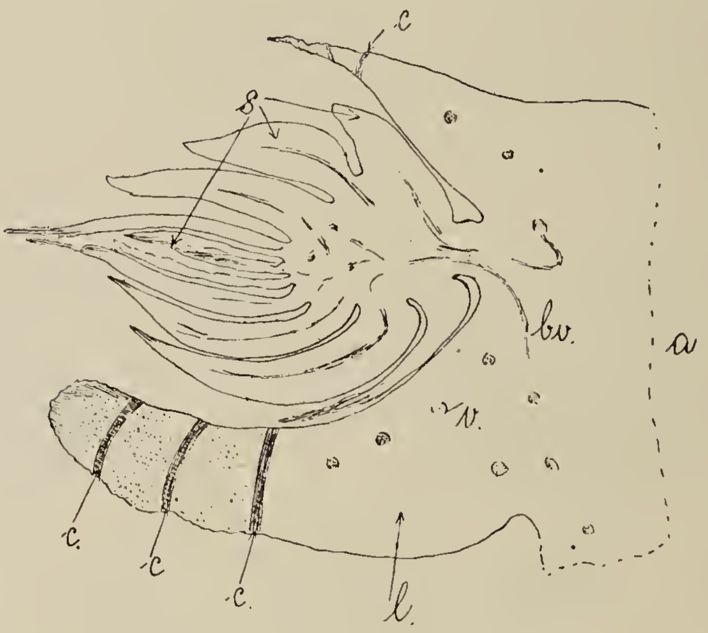

Fig. 12.

Fig. 11. Sketch of one of the irregular roots which stand out externally from the buds growing on the leaf-bases. Some roots like this tend to penetrate the bases again after growing for some time in the air. *l*, end cut off from the "bud," *t*, smooth tip standing out in the air.

Fig. 12. Diagram of a section through a "bud" and the leaf-base from which it has arisen. *a*, axis of parent plant. *l*, leaf-base with zones of cork *c*, and vascular bundles *v*. *bv*, bundles running out from the "bud" and dying away in the leaf-base. *s*, scales of the "bud."

Series of sections show that the "buds" are really attached to the leaf-bases. They arise in general on the upper surface of the base and grow directly upon it with no root or even definite constriction. The vascular cylinder of the bud tends to run through the flesh of the leaf-base for only a short distance, but may even penetrate an adjacent base. In any case it soon dies out, sometimes without seeming to connect definitely on to any of the vascular strands of the leaf-base. The diagram in Fig. 12 shows the attachment of such a "bud." This drawing is made from a longitudinal section through the whole structure.

The "bud" here has a slight constriction at the base, which carries it out a little from the leaf-tissue on which it is seated. Such an axial portion is clearly seen also in the larger "bud" illustrated in Fig. 9 (iv), *s*. The "buds" are generally entirely sessile however. The vascular strand running up each of them, and in the bases immediately below, is circular, with a fair development of wood in the case of the larger "buds." This strand does not continue very far in the tissues of the leaf-base and seems to end there blindly while the buds are still small.

"Buds" like that shown in Fig. 9 (iii) are much more rare. As seen in the figure, it is attached rather laterally to the parent leaf-base, see B., Fig. 9 (iii) and the "bud" with its root looks very like a seedling with a thick primary root and a sucker on one side. Although there was no opportunity for making experiments with the living plants, it seems likely that these are the buds which might be detached and grow independently.

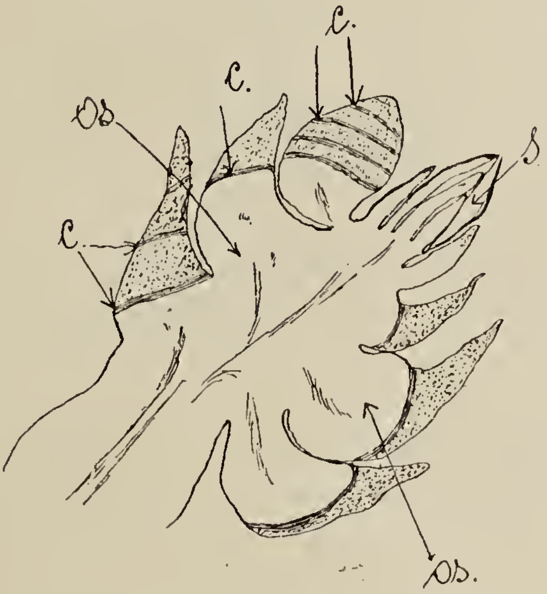

Fig. 13. Longitudinal section through one of the "buds" which has persisted for a long time. *s*, fresh apical portion; *os*, old outer scales with decaying tips cut off by zones of cork, *c*, and with thick bases packed with starch.

Comparatively few large roots such as are figured in Fig. 11 are to be found on the trees. Their behaviour is uncertain, and in several instances I noted that they penetrated the leaf-bases again after running for two or three inches in the air.

The structure of the "buds" themselves has been indicated already in the figures. A young "bud" such as is shown in Fig 9. (i) *s*, is composed of only two or three soft scales, but the older "buds" are well armoured as they are exposed and seem to be prepared to spend a long time dormant. The outer scales are very hard and spiny and the inner, unfolding ones are covered with dense hair. They reach a considerable size, double that shown in Fig. 9 (iv) before they unfold the small green foliage leaves (cf. Fig. 14, *b* and *c*) which appear in the development of active buds, but these are laid down while they are still about the size of the "bud" in Fig. 9 (ii).

Many of the small "buds" show signs of having been vegetating between the leaf-bases for a long time, and their outer scales are much blackened and dried up. Such a one is shown in Fig. 13 cut in longitudinal section. This diagram shows the small fresh apex *s* and the old scales behind it which have become very thick and fleshy. The latter are filled with starch at the base, and the decaying tips are cut off by several successive zones of cork, *c*.

The power to cut off almost any part of its tissue and grow behind the separating layer is a remarkable feature of the Cycads. Solms Laubach[1] noted the persistency of the leaf-bases, and figured some which are cut off by three successive layers of cork; while even the seeds will continue to grow[2] when the internal aborting portions are cut off by a corky layer. This power serves the "buds" in good stead and enables them to linger on almost indefinitely.

These buds have so far been described merely as phenomena interesting in themselves. Their real importance, however, lies in the fact that they appear to be the clue to the real nature of most of the "branching" in *Cycas*. Without overlooking the possibility of other methods of branching, the behaviour of the buds makes it clear that probably the great majority of "branched" plants are simply those in which one or more of these adventitious "buds" developed from the leaf-bases, had grown till it rivalled the main axis. Such plants as the one figured in Fig. 14 are exceedingly common in Japan, and show the stages of the process.

The Japanese pot specimen figured by Wieland (*loc. cit.*) in his Fig. 10, p. 39, as a hoso-type will be now recognised as an excellent example of the branch-forming growth of these buds. While such plants are much cultivated by Japanese gardeners, they also nip off the buds and grow them as independent plants.

Once my attention was attracted to these buds I found that they were almost universal in the older specimens of *Cycas* in Japan, and that nearly every "branch" showed signs of having arisen in the beginning from one of them. According to the position of the prospering bud, the kind of branching varies, and when the bud develops near the apex, once it has reached a diameter comparable to that of the main stem, it gives the plant much the appearance of a dichotomous trunk. When the "bud" increases to such an extent of course, strong woody connections are formed with the main axis, and the leaf bases on which it originated are crushed back, so that the mature appearance of the plant is identical with what it would have been had the axis itself branched, and may well deceive anyone into believing this to be the case.

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[1] Solms Laubach, Graf zu. "Die Sprossfolge d. Stangeria u. d. übrigen Cycadeen." Bot. Zeit., 1890, cf. p. 226, Taf. II., Fig. 2.

[2] Stopes, M. C. "Beiträge z. Kenntnis d. Fortpflanzungsorgane d. Cycadeen," Flora, 1904, cf. p. 446 and 453.

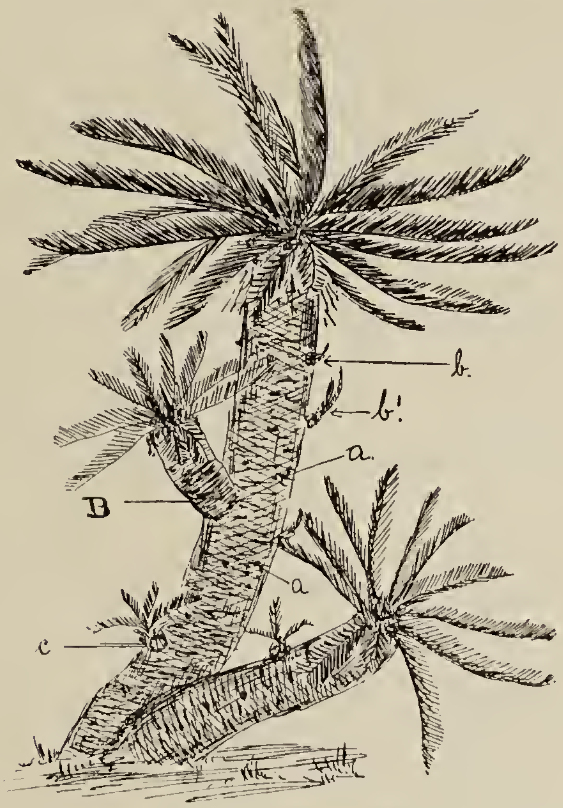

Fig. 14. A *Cycas* showing the beginning of the so-called branching. At *a* are the small "buds" between the leaf-bases. At *b* one enlarged, at *b* (i.) one bearing a few foliage leaves. A large "bud" with a full crown of leaves is seen at *c*, while it is evident that the "branch" B is simply a further growth of a "bud" similar to *c*.

These observations were made while travelling in Japan with a Grant from the Royal Society, which, though allotted for other work, was the means of bringing about the present minor investigation.

The University, Manchester.

THE RHIZOPHORE OF *SELAGINELLA*.

By W. C. Worsdell.

[Text-Figs. 15, 16].

My recent observation of abnormal forms of the rhizophore in various species of *Selaginella* has led me to write on the subject of the morphology of this organ, about which there has been so much controversy and divergence of opinion.

The rhizophore of *Selaginella*, the tubers of Dioscoreaceæ, the submerged vegetative portion of the plant-body of *Utricularia*, the ovule of the Angiosperms, and the sporangium of the Vascular Cryptogams are examples of organs, the ascription to which, owing to their peculiar structure, position, &c., of a place in any one of the usually accepted morphological categories of shoot, root and leaf has always been a matter of considerable difficulty; and this difficulty has been for some botanists so grave that they have, as it were, cut the Gordian knot and placed the doubtful organ in a new category, the characteristics of which are those of the particular organ itself!

But the view that there can exist at the present day, at this very late period of plant-evolution, organs which are *still*, so to speak, undifferentiated, or that any group of plants can give rise to *new* organs which represent in themselves a *fusion* of distinct types of organs which have already, time and again, been evolved during the past history of the race,—is to my own mind in the highest degree improbable. If we consider, for present purposes, the vegetative organs alone, we find that the tendency in all groups of plants, except those which, like the Fungi, have become adapted to a saprophytic or parasitic mode of life, is towards the differentiation of the plant-body into three, and three only, stereotyped sets of organs resembling what we are accustomed to speak of as *shoot*, *leaf*, and *root*. The highest forms in the three great classes of Algæ shew this tendency. It does not tell against, but in favour of, my view that here and there in the Algæ there is no sharp distinction between shoot and leaf, for it is precisely in this group that the evolution of this differentiation has taken place. Indeed this group represents the foundation upon which all higher groups have been established, and it is only what we should expect that here and there the distinction between shoot and leaf is not an *obvious* one. Such a resemblance between the two categories of organs, we should, however, never expect to find in any group higher than the Algæ;

and these expectations are clearly fulfilled in forms where the homogeneous thallus of the lower forms has become thus specialised. The same is true of the Lichens. Again, the highest members of the Bryophytes, show the same intricate specialisation. In all Vascular plants precisely the same primary differentiation into shoot, leaf, and root occurs; we find these three organs universally distributed and each under such manifold forms, shewing evidence of having undergone such profound and varied modification, that we feel compelled to refer the origin of each organ to the very beginning of the evolution of vascular plants.

Thus, from the primitive undifferentiated thallus out of which all plants have been evolved, there has proceeded, in *all* groups, as well in the gametophyte as in the sporophyte generation, a perfectly well-defined differentiation of the plant-body into three stereotyped, fixed categories of organs, *viz.*, shoot, leaf, and root, *and into none other.*

There can be no room in that region of the vegetable kingdom above the level of the homogeneous thalloid types for any organ which is neutral, intermediate or undifferentiated in character, for the preservation of any such organ is, as we have seen above, contrary to the whole trend of evolution, and there is no evidence for the existence of any such organ amongst the simpler types where we should first of all expect to find it. In these lower types, no matter in what group—Algæ, Lichens, Bryophytes or Vascular Plants—we may choose to look, there exist the three organs: shoot, leaf and root, or their analogues, and (confining the discussion to the vegetative region, to which the rhizophore, which I shall hereafter treat of, belongs) it seems impossible to discover any other organ but just these three.

Supporters of the idea of the homologous alternation of generations, however, hold that certain organs, *e.g.*, the sporangiophore of the Pteridophytes, the rhizophore of *Selaginella*, the Stigmarian axis, may have originated as a specialised portion of the thallus of an Alga or Bryophyte before the categories of stem and leaf were differentiated. If the homologous alternation view is true, this may have been so, but is most unlikely. I cannot, however, here enter in a discussion of this view, as it would involve that of the whole question of alternation of generations, with regard to which I refer the reader to the literature on the subject. It is enough to say that in the present paper I write as a believer in the antithetic alternation of generations.

The only other alternative to the view above set forth is that a given group of plants, or small section of a group, could evolve independently, on its own account, a *new* type of organ, possessing

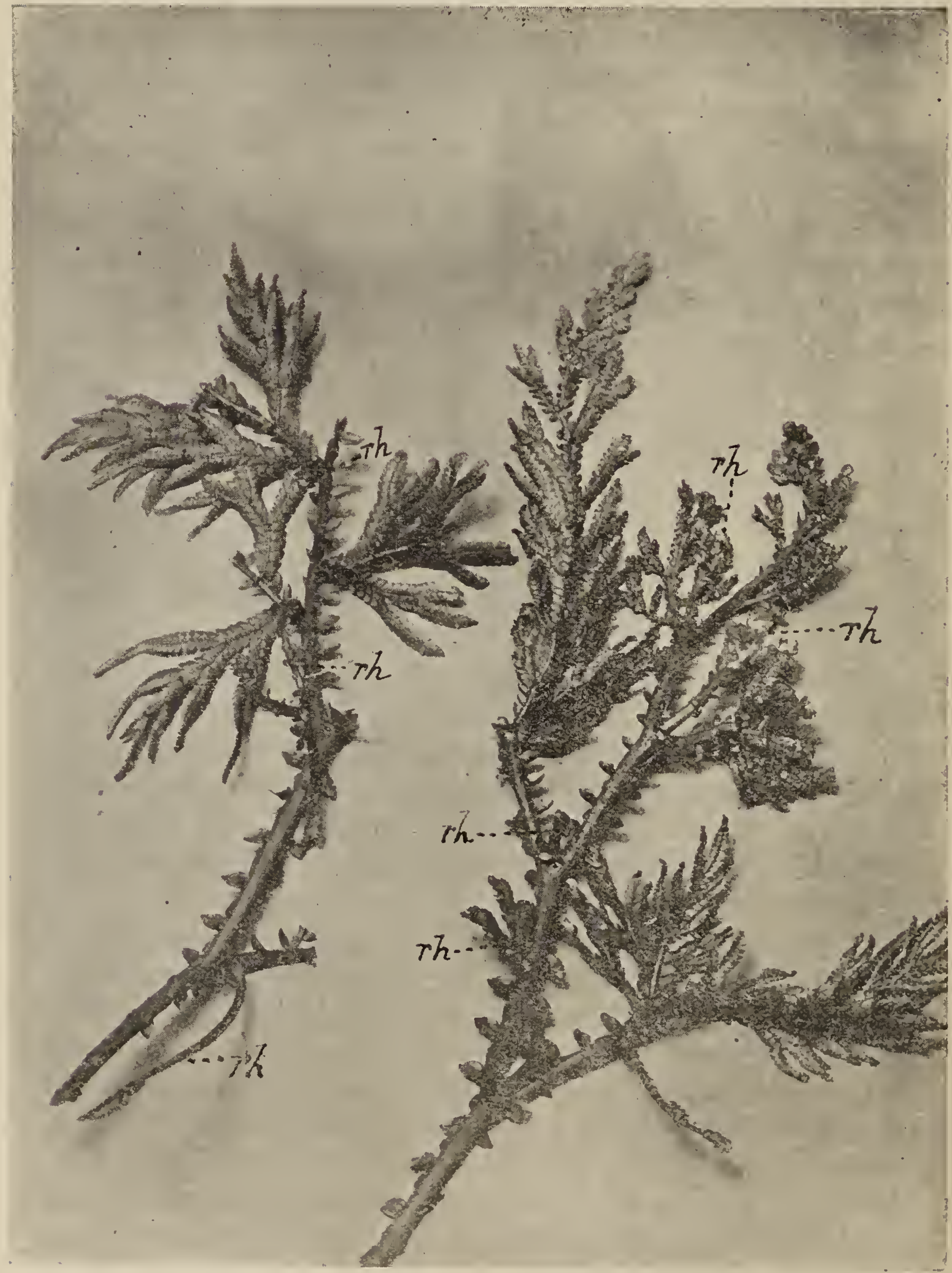

Fig. 15. Photograph of portions of two shoots of *S. inequalifolia* shewing rhizophores arising at the points of forking.

special and distinct characteristics which are not referable in their entirety to any of the existing types. Now, the organs whose morphological value and origin are doubtful or unknown, are *in a very small minority* (I have cited most of them above). I ask, therefore, which is the more likely theory: (1) that certain *specialised* groups have produced new types of organs after the lapse of an immemorial past of evolution in which we can find no trace of such, or

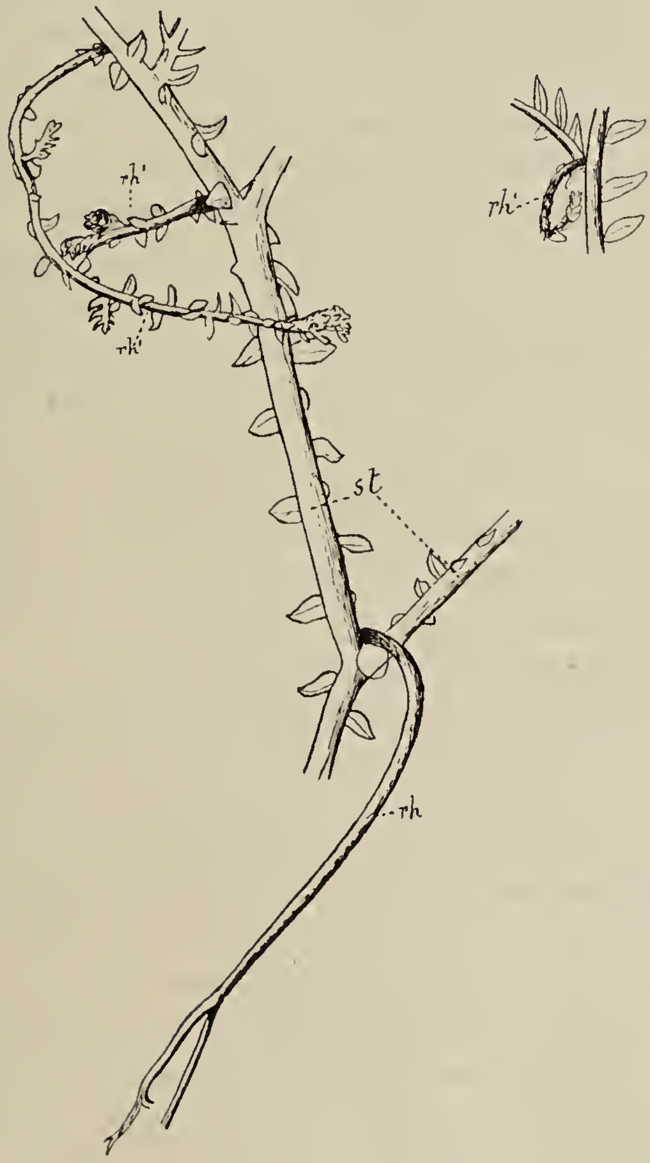

Fig. 16. Portion of shoot of *S. inequalifolia* shewing rhizophores arising at points of forking.

(2) that here and there in certain groups some already-existing organs have become specialised and modified to such a degree as to render them no longer recognisable as such, and hence, *apparently* new and distinct in type? For my part, the second of these hypotheses is the only tenable one.

The facts cited above go to shew that there can be no organs at the present day which are intermediate in essential nature between root and stem or between stem and leaf, &c., but that there *may be* organs which are intermediate *in appearance*, through possessing some of the characters which are typical of quite distinct organs. But it is one thing for organs (*e.g.*, root and shoot) which have for ages been differentiated as such to become *apparently* fused, or indistinguishable on the surface (owing to extreme specialisation as the result of adaptation to special functions), and quite another thing for those same superficially-doubtful organs to represent a persistent, undifferentiated, neutral type or a completely new departure in the form of something *sui generis*. I am unable, therefore, to accept or understand the position maintained by Goebel and others that such indifferent *sui generis* organs can and do exist. Nor can I concur with the method of classifying doubtful organs (such as the tubers of Dioscoreaceæ and the rhizophore of *Selaginella*) *in terms of the mere appearance which such organs present* (*as regards structure, habit, position, &c.*) *to ordinary observation.* I conceive it to be the duty of the morphologist to set himself firmly against any purely *descriptive* method of the classification of structures, his ambition rather being to reach beyond the mere appearance and to fathom, if possible, the real nature, *i.e.*, the phylogenetic origin, of the structures concerned.

The *rhizophore* is an organ confined to the genus *Selaginella*. It occurs, either on the upper or lower surface, or both, at the point of branching, of the (usually) dorsiventral stem, and subsequent in time to this branching. It rapidly elongates into a root-like organ which grows downward to the soil, on reaching which, or slightly before, it emits roots close behind its apex which serve to fix the plant in the substratum. The rhizophore usually dichotomizes before reaching the soil. It is probable that all species produce rhizophores and under normal circumstances, it is only through the indirect method of rhizophore-formation that roots are ever produced. It has been shewn, however, that roots can be induced to form *directly* from the basal ends of stem-cuttings, and the much swollen base of the hypocotyl of *S. spinulosa* also produces endogenous *roots* directly.

The question is: what morphological value has the rhizophore? for that it must represent either a root, a shoot or a leaf follows from what I have already written above. For obvious reasons it cannot be a leaf. It is therefore either a root or a shoot. It resembles the root of the same plant in the anatomical structure of its vascular parts, for it has a monarch structure of the stele with central protoxylem. Like a root, it is completely devoid of any lateral appendages in the form of foliar organs. Like a typical root it grows *downwards* to the soil and absorbs water through its tissues in a direction the reverse of that in which it has grown. It produces lateral endogenous roots. These characters are, in my opinion, not sufficient to warrant us placing the organ in the root-category. On the other hand it resembles a stem or shoot in the fact that it arises *exogenously* from the tissue of the leafy shoot at the region of forking; but this in itself is not conclusive evidence in favour of its stem-nature, for exogenous roots are known in various plants. But as Bruchmann points out, the *definite* place of origin of the rhizophores at the place of forking, growing in a plane at right angles to that of the stem-fork, the whole forming a cross-like four-armed branching-system at that point, speaks strongly in favour of these organs being shoots. The absence of a root-cap is another character speaking in favour of its shoot-nature. The leafless character affords no argument against this idea; several cases are known of shoots which have for the purpose of some special function, lost the power of forming leaves, either over the whole or a part of their length, *e.g.*, the rhizomes of Psilotaceæ, the inflorescences of Cruciferæ, the shoots of *Trichomanes membranaceum*. The anatomical structure is known to be a varying factor and is totally unreliable as an absolute determinant of the stem- or root-nature of an organ. For instance, the rhizome of *Trichomanes muscoides* has a monarch stele-structure just like that of the rhizophore of *Selaginella;* it has obviously been derived from the structure of other species by reduction of the metaxylem; in the same way the rhizophore-structure could easily be obtained by reduction of one half of the xylem of the diarch stem-stele of a form like *S. Martensii*, along with elimination of the phloem on the outside of the protoxylem which is preserved. It is thus apparent that the stele-structure stands as a very small point in favour of the root-nature of the organ. It is only what we should expect, that the downward-growing direction, the leafless character, and fixation of the apical end in the soil should induce a root-like structure of the stele of an organ which was originally of shoot-nature.

Pfeffer has placed on record some most interesting observations in which rhizophores of certain species (e.g., *S. inequalifolia*) develop spontaneously into *leafy shoots*.

I have myself recently observed the same phenomenon in the case of the above-mentioned species in the Fern-house at Kew. In the case of one shoot which I may take as a typical example, of the two rhizophores at one fork of the stem, that on the lower surface was perfectly normal and elongated, and with the usual dark-brown colouration, the upper one was very short and changed into a leafy shoot; at the next node the upper rhizophore was a leafy shoot and growing almost horizontally: at the next the lower rhizophore was much elongated, growing downwards, and with leaves somewhat sparsely scattered along its whole length; the tip was becoming green, the rest being dark-brown, and it was just beginning to bend upwards, while at intervals along its course it bore a short leafy branch (this rhizophore represents an interesting transitional form between the normal organ and the rhizophore transformed into a leafy shoot); at the next node the lower rhizophore is a very short leafy shoot and there is no upper one; at the next the only rhizophore present, *viz.*, the lower one, is a leafy shoot which at first began to grow downwards but soon bent upwards sharply; it therefore also represents a more or less intermediate stage of transition.

On other shoots the transformed rhizophores were much less half-hearted; many of them at once grew quite vertically upwards into typical leafy shoots, each arising at the point of forking of the normal stem; the extreme base of these "rhizophore shoots," for a distance of 2 or 3 mm., is dark-brown and leafless like the normal rhizophore. This dark-brown colour *gradually* merges into the green of the typical normal shoot.

In a panful of *Selaginella Mettenii*, A.Br. (a garden hybrid) I noticed that in most, if not all, the plants normal rhizophores were only formed in the *lower* part, where the plant was moist and shaded; in the upper part the rhizophores were invariably replaced by typical leafy shoots which appeared always on the upper surface of the stem; I saw no transitions between them and rhizophores, but their position shewed clearly that they represented the latter.

I have also observed rhizophores in the form of leafy shoots in the following species, besides the two above-mentioned: *S. Wildenovii* Baker, *S. canaliculata* Baker, *S. serpens* Spring and *S. grandis* Moore. In the first-named I saw a rhizophore in the form of a branched leafy shoot quite a foot high; in the last-named (*S. grandis*) they are in the form of small, flower-like structures, as described by Goebel.

Bruchmann found in the case of S. *Kraussiania* A.Br. that by cutting off the two arms of the stem-fork at an early stage of the development of the rhizophore, *i.e.*, before the initials of the endogenous roots are laid down, the apical cell of the rhizophore becomes that of a leafy shoot and the latter becomes the direct continuation of the former. If, however, the root-initials have already been formed then the leafy shoot arises laterally and below the root-initial, and presses the rhizophore-apex to one side, and the latter eventually shrivels up. This phenomenon may, I think, be explained on the assumption that, after the root-initials are laid down, the rhizophore-apex has become specialised and differentiated to form a kind of pseudo-rootcap or protective covering of the region where the young roots are forming, and hence has lost the potentiality of developing into a leafy shoot. I myself performed a similar experiment to that of Bruchmann with stems of S. *inequalifolia* and S. *Mettenii*, and with similar results. From all the above-cited facts it is clear that the leafy shoot in these cases arising on the upper or lower surface of the dorsiventral stem at the base of the fork is itself a rhizophore; the appearance suggests unequivocally that the phenomenon before us is *not* a case of a normal rhizophore being first formed which then gives rise by transformation of its apex, to a leafy shoot; on the contrary, it is clear from direct observation that there is only one organ here present. The cases of *Neottia*, *Listera* and *Anthurium* are not to be regarded as parallel, for in these there was a clearly-defined organ, *viz.*, the root present in the first instance, whose tip developed *suddenly* into a leafy shoot, without any transition whatever between the latter and the root; it is most obvious that there are two distinct organs present: the terminal shoot in these cases is almost certainly an adventitious structure which, at first in its origin lateral, has encroached ever more nearly to the apex until it has entirely usurped the latter. No interpretation of this sort can be placed on the phenomena in *Selaginella* above described. My observations seem to prove unequivocally that *the normal rhizophore has the morphological value of a shoot.*

Bruchmann caused, in rhizophores whose tips had been cut, the formation of fresh roots from the callus. He also induced the formation of roots from the ends of stem-cuttings.

This author has now established that, in the case of *all* species of *Selaginella*, including S. *Martensii* (the species investigated by Pfeffer) there is (in spite of what Pfeffer described) no radicle or primary root present; but from the base of the elongated hypocotyl two to three *short* rhizophores develop, and it is indirectly and endogenously from these that the first roots arise. Goebel compares this "outgrowth," as he calls it, from the hypocotyl with the "protocorm" of the seedling *Lycopodium*.

In *Lycopodium*, indeed, the morphology of the seedling is not at all dissimilar to that of *Selaginella*; the hypocotyl is, however, reduced to a minimum and developes at once into the "protocorm," a tubercle-like body bearing rhizoids. It is only at a subsequent period that the first root is formed endogenously or exogenously from the "protocorm." From the above facts it seems to me highly probable that the rhizophore of *Selaginella* and the so-called "protocorm" of *Lycopodium* are homologous structures; and if, as I am quite convinced, the rhizophore is morphologically a modified shoot, then it follows that the "protocorm" is also a highly modified shoot; and there is nothing on *à priori* grounds to render this conclusion improbable.

Now Lang found that in the saprophytic species of *Lycopodium*, e.g., *L. clavatum*, the "protocorm" is absent and the primary root developes directly from the base of the hypocotyl. He states that the type of *L. cernuum*, with large prothallus and well-developed "protocorm," is the *primitive* type. In *L. Phlegmaria*, only a degree less primitive, the protocorm is only just distinguishable. Hence I conclude that in the saprophytic forms the "protocorm" has merely been *reduced* to a vanishing point, just as the hypocotyl also, as compared with that in *Selaginella*, has practically gone. Nevertheless, the basal part of the young plant must be homologized with a "protocorm" out of which the root grows. Bruchmann's investigations of seedlings of *Selaginella* shew that Pfeffer, Campbell, Velenovsky and others are mistaken in supposing that a primary root is present at all in this genus; Velenovsky figures seedlings of *S. pumila* and *S. Preissiana* in which the primary root, according to his account, has arisen *endogenously* from the hypocotyl, which seems to indicate that the extreme basal portion of that organ is, in reality, a rhizophore, which has, like the "protocorm" in certain *Lycopodiums*, almost reached its vanishing point.

It is in *Phylloglossum* that the "protocorm" reaches its best development.

By keeping a shoot of *S. Mettenii* in a moist atmosphere I was able to induce *normal* rhizophore-formation in the upper part which usually produces leafy shoots in place of rhizophores (*i.e.*, in the

Kew specimens). Out of three organs which appeared, and which soon began forking, *one* was densely covered with root-hairs, no trace of which could be seen on the other two, hence this particular organ was in all probability a *root* and, to judge by the known facts in other cases, was probably borne on an exceedingly short rhizophore. But I did not investigate the matter more closely. The presence of rhizoids (root-hairs) on the "protocorm" of *Lycopodium* does not, as Velenovsky maintains, necessarily support the idea that this organ is a root, for rhizoids occur on *rhizomes* of Psilotaceæ and Hymenophyllaceæ; it is also an interesting fact for the comparison between the "protocorm" and the rhizophore that Bruchmann observed and figured a rhizophore, produced from the hypocotyl of *Selaginella Martensii*, which bore rhizoids at its tip before the period at which the root-initials were laid down.

When it first became evident to me that the rhizophore was of shoot-nature, I began to ask whether its position on the stem was in harmony with this conclusion. In 1892 Velenovsky discovered, for the first time in the vegetable kingdom, the phenomenon of *tetrachotomy* in certain species of *Selaginella*; this consists in the presence immediately below each fork of the stem of two smaller shoots, one on the upper and the other on the lower side of the axis; in fact, the stem here branches apically into four arms, all of equal value and two of which are in a plane at right angles to that of the other two and are shorter and later in appearance. Now these latter occupy the precise position of rhizophores and are, indeed, nothing else but rhizophores in a different guise. Hence we may conclude that in a typical *Selaginella*-stem the two rhizophores of each fork represent the two delayed and highly-modified arms of the tetrachotomous branching. Their very *definite place of origin* speaks strongly in favour of their shoot-nature. Indeed, there can be no doubt about it after *all* the facts are taken into consideration.

As for the fossil organ *Stigmaria* belonging to the stems of the Lycopodiaceous genera *Lepidodendron* and *Sigillaria*, from what we know of its habit and structure, it is quite likely homologous both with the rhizophore of *Selaginella* and the "protocorm" of *Lycopodium*. The organ under these three differentiated forms which can be given no distinctive name itself (although we recognise its probable shoot-nature), must be extremely ancient, even in its highly-modified form. But we should not wonder at finding highly-differentiated structures and organs in Palæozoic times; the world was probably ancient enough even then.

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NOTE ON A WOUNDED *MYELOXYLON*.

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[Text-Figs. 17, 18a, 18b].

THE question of the powers of healing and of wound tissues generally in Cryptogams, and indeed in all groups below the Coniferæ, seems to have received scant attention, a fact perhaps partially explicable by their lack of economic interest.

Even where mentioned, as in Goebel's "Organography" or Masters' "Teratology," the case of insect wounds or wounds of a very severe character (*e.g.*, amputations) are alone touched upon. In the case of fossil plants the paucity of material, and especially of material in an adequate state of preservation, has rendered any addition to the known records of wounded tissues of peculiar interest.

Up to the present there are, as far as can be ascertained, only three known cases, namely one mentioned by Professor Seward, in the first part of his "Fossil Plants," one by Dr. M. C. Stopes, both dealing with wounded Calamite stems, and the case, recorded in a previous issue of this Journal, by Professor Weiss, of a wound tissue in a Stigmarian rootlet, developed as a result of the attack of a fungal parasite.

It is thought, therefore, that the present instance, coming, as it does, from a group from which no previous cases have been recorded, may be a useful addition to the subject.

The petiole to be described in the present paper was discovered whilst examining the "Myeloxylon" slides of the "Cash" and "Hick" collections in the Manchester Museum and is, unfortunately, represented only by a single transverse section (R 677) cut from material obtained at Moorside, Oldham. As a consequence any conjecture as to the extent of the injury would be fruitless.

The petiole, which is roughly pear-shaped in section, measures across its widest part fifteen millimetres by nine millimetres, and shows the typical Myeloxylon structure, possessing a fairly large pith surrounded by a series of vascular bundles and secretory canals and showing at the periphery the usual alternating bands of parenchyma and sclerenchyma with some traces of a more delicate external tissue.

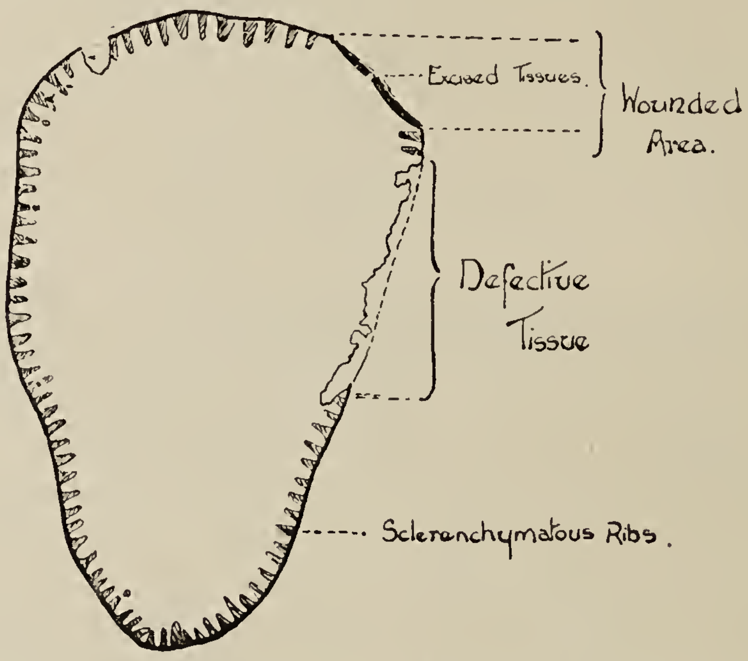

Fig. 17. Camera-lucida outline of petiole showing wounded area and general shape. The sclerenchymatous ribs are represented diagramatically and the vascular bundles and mucilage canals are omitted.

The wound itself shows as a flat, or perhaps slightly incurved portion about four millimetres in extent, and is situated at one corner of the broader extremity. It occupies, roughly speaking, one ninth of the circumference of the petiole, and was therefore of not inconsiderable extent. It does not appear, however, to have been of a really severe nature, penetrating little below the fibrous strands of sclerenchyma and not encroaching upon the vascular structures, a feature in which it differs very considerably from the gaping wounds recorded by Stopes and Seward respectively.

It is not at all likely that it was due to fungal agency, since there is not the slightest trace of any structure which could be construed in that light nor does the general appearance favour that idea.

The great feature of interest, whatever the cause of injury, lies however, in the attempt at repair made by the tissue in the vicinity of the wound. Here the whole of the uninjured cortical cells for quite a considerable depth have become meristematic, their activity resulting in the production of a typical wound cambium.

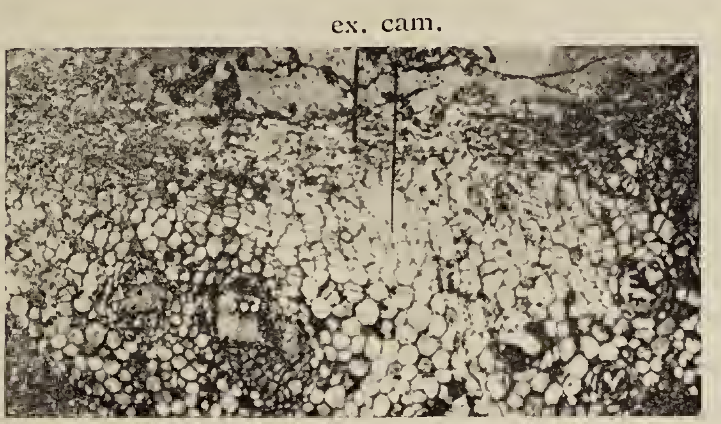

Fig. 18A. Photomicrograph of wound showing excised tissue (ex.) and cambium (cam.).

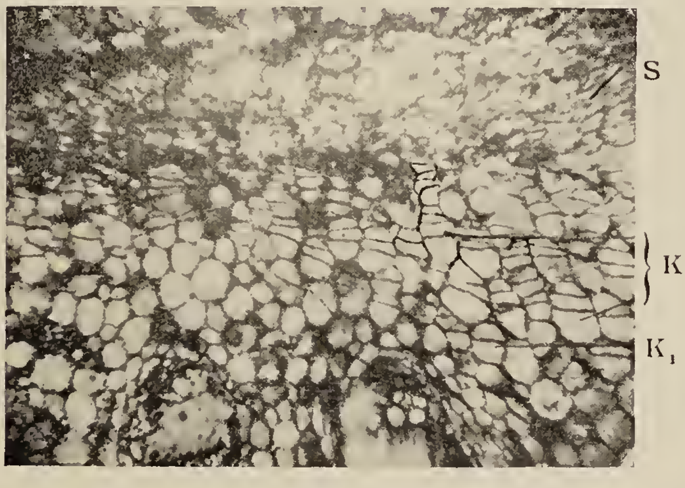

Fig. 18B. Portion of 18A more highly magnified. Note the division of the cortical cells at (K) and (K¹) and the dead suberised cells at (S).

The actual exterior of the wound is naturally occupied by the shrivelled and partially disintegrated tissues originally situated in that position, and without doubt corresponding to the dry brown mass of dead tissue which is produced when an ordinary fern petiole is grazed. Where still distinguishable, the tissues composing this appear to be parenchymatous in character, it being highly probable that the more resistent fibres were torn bodily away by the cause of the injury.

Situated immediately below this strip of ruptured tissue are several rows (from two to seven) of perfectly regularly arranged tabular cells, probably already suberised and devoid of contents, and on the whole sharply delimited from the former. They are very similar in appearance to a true periderm such as is found in the early stages of cork formation in woody dicotyledons or perhaps even more closely resembling the tissue situated immediately below a lenticel. This appearance suggested the possibility of the structure actually representing a lenticel, but the fact of its being the only case recorded of cambial tissues in a Medullosan petiole is all against this view, and a comparison with the lenticels found in the Marattiaceæ and Cyathaceæ again shows very little similarity. It will thus be seen that this view is untenable and that the only one in accordance with the facts is that it represents a true periderm. It would thus appear that these series of cells, which become successively less compressed as they get more distant from the periphery, are the result of the continued division of the cortical cells immediately below the seat of the injury, a feature which one might expect since the plant, to avoid excessive loss of water would naturally produce a layer of protective tissue in that region, as rapidly as its abilities permitted it to do so. Below this layer the original cortical cells are still, in places, distinguishable, but are subdivided into groups of from three to five cambiform cells still forming an almost continuous band of meristematic tissue (Figs. 18A and 18B).

Proceeding ftom the seat of injury towards the centre of the petiole it is seen that the continuity of this zone becomes more and more interrupted until it is represented by an isolated cortical cell here and there showing subdivision into two parts only, and about the region of the first bundle-ring all evidences of abnormality disappear.

Cases of periderm formation among the Ferns are apparently somewhat rare, but they are referred to by Brebner who records them for the Marattiaceæ and also in a later paper by Chandler, the latter of whom gives a figure. A comparison of this with the one forming the subject of the present note reveals a striking similarity, though the cases are not absolutely parallel, since the former (Ann. Bot., XIX., Pl. XX., Fig. 208) represents a typical case of periderm formation in a rhizome, not a petiole. Periderm is also mentioned as occurring in the case of wounds in the rhizomes of the Ophioglossaceæ by De Bary in his opening paragraph on "Cork-formation," and also by Holle.

In conclusion the writer's acknowledgements are due to Professor F. E. Weiss, for much kindly help, to the Museum authorities for permission to describe the slide, and to Mr. Alex.

Mee who has obtained the photomicrographs reproduced as Text-figures 18A and 18B.

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TWO EMBRYO-SAC MOTHER-CELLS IN THE OVULE OF *FRITILLARIA*.

[TEXT-FIG. 19].

WHILE engaged with the sorting and arrangement of the collection of slides illustrating nuclear division in the Botanical Department of the University of Bristol I found one slide of *Fritillaria messanensis* showing the presence of two embryo-sacs in one ovule.

As cases showing this condition are comparatively rare in Monocotyledons it was thought worthy of notice.

Reference has already been made to a similar condition in *Lilium longiflorum* by Miss Margaret C. Ferguson[1]. In her note she describes as the earliest case mentioned the observation of Guignard[2] on *Ornithogalum pyrenaicum* where two archesporial

[1] Ferguson, Margaret C. "Two embryo-sac mother-cells in *Lilium longiflorum*." Bot. Gaz. 43, 1907, p. 418.

[2] Guignard, L. "Recherches sur le sac embryonnaire des Phanérogames Angiospermes." Ann. Sci. Nat. Bot. sér. VI. t. 13, 1882, p. 136.

cells were found. Other cases mentioned in this note are *Lilium philadelphicum* with three and five archesporial cells found by Coulter and Chamberlain[1] and that mentioned by Bernard[2] in *Lilium candidum* where two embryo-sacs, showing the stage with four nuclei, were found lying side by side in intimate contact along their inner faces. He thinks from their appearance they may have arisen by division of a single archesporial cell.

The case described by Miss Ferguson, however, shows two distinct archesporial cells separated by a layer of tissue of the nucellus. They are surrounded by the usual single layer of outer cells of the nucellus, and normal integuments are present. The nuclei as figured show the chromatin thread and nucleoli in resting condition before commencement of the meiotic division.

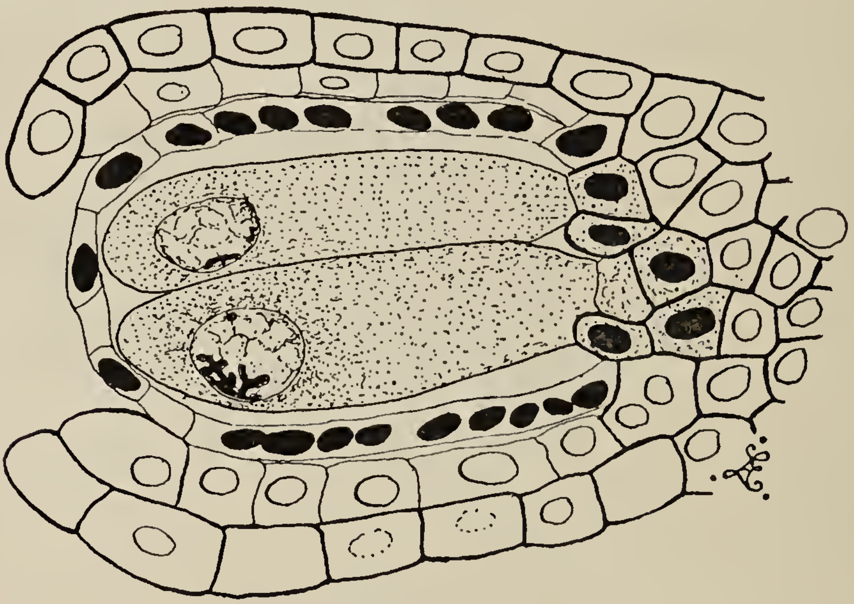

Fig. 19.

The case now to be described shows an intermediate condition between the cases described by Bernard and Miss Ferguson.

In this case the two embryo-sac mother-cells are seen lying side by side in close contact along their inner faces, but with a distinct wall between them.

The two embryo-sacs seem from their appearance to have originated from two distinct archesporial cells. They are enclosed by the usual single layer of cells of the nucellus, and the ovule has normal integuments. The nuclei show the stage following synapsis, the spireme thread has broken up into chromosomes previous to the arrangement on the equatorial plane. The section is, unfortunately, rather oblique and only one nucleus can be seen in detail, but it must be inferred that each nucleus will show the same condition, and as the stage shown by the one nucleus is that previous to the reduction division it is obvious that each embryo sac must have arisen from a separate archesporial cell, as in *Fritillaria* the first division of the nucleus of the archesporial cell is the reduction division.

[1] Coulter and Chamberlain. "Morphology of Angiosperms." New York, 1903, p. 61.

[2] Bernard, C. H. "Recherches sur les sphères attractives chez *Lilium candidum*." 1900. Jour. de Botanique 14, p. 178.

When early stages of the megasporangium of *Fritillaria* and *Lilium* are examined it is seen to consist of a mass of cells, the nucellus; the cells can be distinguished by their large nuclei and dense protoplasmic contents. Any one of the more central cells can function as an archesporium and all may be considered potential archesporial cells. Although normally only one cell functions as the archesporium, yet all the cells adjacent to this one must be under very similar conditions, and a case might easily occur where more than one might function. There seems no reason to suppose that should this occur two complete embryo-sacs would not be formed, although this state has not yet been observed.

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April, 1910.

THE BRUSSELS CONGRESS OF BOTANISTS.

THE Third International Congress of Botanists was held at Brussels from May 15th to the 22nd in the present year. Apart from the work of the sections, the Congress afforded a very pleasant and profitable opportunity for the botanists of all nations to become personally acquainted. The city of Brussels is a most attractive meeting place and occupies a fairly central position, especially for the botanists of Northern Europe. There was a good attendance of representative men. The General Secretary of the Congress was M. de Wildeman.

The meetings of the sections, apart from the formal opening session, which took place at the well-known Botanic Garden in the centre of the city, were held in the Exhibition Buildings, close to the Bois de Cambres, a considerable distance away, and the necessity for going to and fro over so long a distance was felt by many members to be inconvenient.

Section of Taxonomic Nomenclature.[1]

The chief work of this section was to complete the Rules passed at Vienna in 1905 so far as concerned special points relating to non-Vascular Cryptogams and Palæobotany. It was generally felt that the "Species Plantarum" was not a satisfactory starting point for many of the lower groups about which little or nothing was known in 1753. The question of separate starting points was therefore considered by the workers concerned with the various groups, and the resulting recommendations were brought before the meetings of the section.

It was decided to go back to 1753 in the case of the Mycetozoa, of most of the Algæ (including Characeæ) and of the Lichens. Later starting points were however agreed upon for the Desmids (Ralfs, 1848), Oedogoniaceæ (Hirn, 1900) and Nostocaceæ, (Homocysteæ, Gomont, 1890, Heterocysteæ, Bornet and Flahault, 1886-88). The rest of the Schizophyceæ with the Diatoms and and Flagellata were reserved for further consideration.

For the Fungi it was agreed to start with Fries' "Systema Mycologicum" (1821-32), except in the case of the Uredineæ, Ustilagineæ and Gasteromycetes, for which Persoon's "Synopsis Fungorum" (1801) was chosen.

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[1] The Editor is indebted to Dr. A. B. Rendle, Mr. H. N. Dixon and Dr. R. Kidston for information on the work of the section.

As regards the nomenclature of pleomorphic Fungi, it was agreed that successive states of the same species should bear the same generic and specific name, to wit, the earliest name given to the perfect state of the fungus in or after the work agreed upon as the starting point, provided that such name otherwise conforms with the Rules. The "perfect state" is defined as that which leads up to the ascus in the Ascomycetes, the basidium in the Basidiomycetes, to the teleutospore in the Uredineæ and to the spore in the Ustilagineæ.

Among the Bryophyta, the Hepaticæ are to start with the "Species Plantarum," as also the Sphagnaceæ, while the rest of the Mosses are to begin with Hedwig's "Species Muscorum" (1801).

Thus the principle of uniformity of starting point has very wisely been sacrificed to the practical needs of workers in the various groups, who have settled the most suitable points of origin in each case.

On the vexed question of *nomina conservanda*, the compromise adopted at Vienna, by which certain very well-established and very well-known names are retained in defiance of the strict principle of priority, was maintained in spite of the opposition of those who hold that no exceptions should be made in the logical application of this principle. Some additions were made to the list, but it was agreed that changes of nomenclature which have already been made in accordance with the Rules of 1905 should not be upset.

The commissions were re-appointed, with alterations and additions for the various groups of Cryptogams, to draw up lists of *nomina conservanda* for each group.

With regard to the nomenclature of fossil plants the starting point was taken, as in the case of most of the recent plants, as 1753, the date of Linnæus' "Species Plantarum." It was also agreed that a plant should be technically considered as "described" when the description is accompanied by a figure showing the essential characters.

It was resolved that all diagnoses should be written in Latin; although it was pointed out that this did not imply a long Latin description, but only a Latin enumeration of the most important characters, the resolution was accepted with the greatest reluctance by the palæo-botanists present. Indeed it is the opinion of more than one distinguished worker in this branch of the science that no attention will be paid to this Rule.

In order to reduce to a minimum changes of name arising from the use of the same name in the nomenclature of recent and fossil plants it was decided to draw up a double list of *nomina conservanda* for the guidance of workers. This is to include (1) generic names of living plants, duly published and in general use, which enter into collision with old generic names in Palæobotany, e.g., *Bucklandia* Br., (2) generic names of fossil plants, duly published and in general use, which enter into collision with older homonyms of living plants that have been relegated to synonymy. The object is to prevent the further use of the names in the second sense in each case.

SECTION OF PHYTOGEOGRAPHICAL NOMENCLATURE,

At the Vienna Congress in 1905 a commission was appointed entrusted with "studying the practical means of directing the efforts of phytogeographers, and of bringing them back, as far as possible, to the observation of nature and to the interpretation of concrete phenomena." Messrs. Flahault & Schröter were appointed Secretaries and were requested by the commission to present to the Brussels Congress a report on phytogeographical nomenclature which would serve as a basis for discussion. The Reporters at once placed themselves in communication with botanists engaged in phytogeographical research, and in the spring of the present year issued a Report representing their efforts to disentangle from correspondence and from published works those elements which they found it necessary to submit for discussion to the Brussels Congress, and embodying also their own matured views and recommendations. This Report is a very valuable document, for it contains not only an able discussion by the Reporters of the principles and practice of phytogeographical nomenclature and cartography, but also a number of recommendations and suggestions sent in by various phytogeographers from Europe and America. The recommendations and suggestions emanating from different workers are however very diverse and in many instances contradictory, and the voting of the members of the commission on certain of them selected by the Reporters and recorded in a document issued at the Congress shows that there is nothing approaching unanimity among phytogeographers on many of the points raised. The recommendations of the Reporters themselves, however, it is fair to add, obtained in all cases a majority of votes by members of the commission, and in several cases unanimous assent.

At Brussels a private meeting of the phytogeographers present was held before the session of the Congress devoted to the subject. The long discussion which took place at this meeting further emphasised the divergence of opinion on several fundamental points, and taking this into consideration the Reporters most wisely refrained from presenting to the Congress any recommendations but those on which they were practically certain of unanimity. The restraint and moderation shown by the Reporters in not pressing even those of their own recommendations on which there was lack of unanimity, though, as shown by the voting of the commission, they would certainly have obtained large majorities, cannot be too highly praised. In the present state of the subject it would be most undesirable to attempt to bind workers even with the loose bonds of "Recommendations" of Congress unless complete conviction is carried as to the scientific and logical validity of the principles involved.

The recommendations actually submitted at the session of Congress on Friday, May 20th, were substantially as follows:—

(1). Every author should state exactly what he understands by the terms he uses.

(2). The native names of different kinds of vegetation belonging to various languages should be retained.

(3). The principle of priority (as recognised in taxonomic nomenclature) is inadmissible in phytogeographical terminology.

(4). A lexicon of synonyms in use in various languages, with bibliographical references to their use, should be compiled by an editorial commission.

(5). Engler's colour scheme for maps of tropical vegetation is recommended for general use.

(6). Ecological phytogeography may be defined as the study of the relations of plants and plant-communities with the environment (*milieu*).

All of these recommendations were voted upon by raising the hand, and were carried *nemine contradicente.*

The Reporters also stated that they had found there was general agreement on the following proposition:—The plant association represents a definite entity in vegetation, while the plant-formation is something different. This proposition was not put to the vote. It may, however, be said that there is almost complete unanimity on the proposition that the plant-association is a unit of definite floristic composition, while the plant-formation represents a unit of a higher category.

It is to be regretted that no agreement was reached on the terminology relating to altitudinal belts or zones of vegetation. The Reporters proposed to restrict the word *zone* to the great climatic zones of the earth as a whole, to adopt the terms *belt*, *étage*, *Stufe* for altitudinal "zones," and to introduce the terms *girdle*, *ceinture*, *Gürtel* for other "zoned" arrangements of vegetation. They recommended that the term *region* should be confined to extensive stretches of country. Prof. Engler opposed this last recommendation on the ground that "region" in the sense of "altitudinal zone" has been used in innumerable phytogeographical descriptions.

Some workers may be disappointed with the comparatively slight progress that has been made towards settlement of the important questions dealt with in the "Report." It must, however, be remembered that while the section of taxonomic nomenclature has to deal with rules which necessarily have a purely arbitrary foundation, and are adopted for the sake of practical convenience, the task of the phytogeographical section is quite different. Phytogeographical nomenclature deals with the *concepts* which form the basis of this branch of the science, and the task set to the Reporters was to find out how far general agreement prevailed as to these concepts. It is useless to recommend the general adoption of terms corresponding to the concepts, unless general agreement prevails as to the concepts themselves. It is evident that in the present state of phytogeography we have not quite reached such a general agreement, and this is not to be wondered at when we consider the unexampled difficulty of properly determining concepts relating to the varied and constantly changing groupings of vegetation.

Meanwhile the thorough ventilation of the questions and the interchange of ideas that has taken place will be of the greatest possible benefit to the science, and the very greatest credit is due to the Reporters for the immense pains they have devoted to the subject, for their able summary of their own views, for bringing together the most important opposing views, for their invariable courtesy and moderation and generally for the statesmanlike manner in which they have dealt with the whole problem.

Excursions.

The excursions organised by Professor Jean Massart were not, for the most part, attended by very large numbers of congressists, doubtless because many of them took place while the Congress was sitting, but those who did attend found them both extremely pleasant and very profitable.

The first excursion, lasting two days, May 12th to 14th, before the Congress, was to the Belgian littoral, where the magnificent sand dunes, with their "pannes" or marshy hollows and their cultivation, together with the salt marshes or "schorres" and the peat-deposits below the "polders" (recent alluvial deposits occupying a considerable area of country in North-west Belgium within the line of dunes), were examined.

On Tuesday, May 17th a party visited the Agricultural Institute at Gembloux, under the guidance of M. Marchal, and afterwards the woods near Mazy on a very rich soil, derived from dolomitic rocks. These woods, which are largely of beech, have a rich and varied ground-vegetation very similar to that which we get in woods on deep calcareous soil in this country.

On Wednesday there was an excursion in the valley of the Dendre, where the flora of sandy banks and arable fields was investigated. In and about alder woods on marshy alluvium *Lathræa clandestina* was most abundant in its northernmost European station on the roots of *Populus monilifera*, *Alnus glutinosa* and *Salix alba*.

On Thursday the sittings of the Congress were suspended, and a large party took train to Tamise and then went down the Escaut by steamer to Bornhem, where the relations of the tides to the vegetation of the river-banks were demonstrated. After examining the plants of the drainage-ditches of the adjoining "polders," the party re-embarked and descended to Antwerp.

On Saturday an excursion was made to the banks of the Meuse at Tailfer and Profondeville, a few miles above Namur. Here the river cuts through lofty cliffs of dolomitic limestone, and the scene is very picturesque. The limestones are interbedded with non-calcareous schists, and the contrast between the vegetation of the two geological formations is very striking. On the sun-baked calcareous rocks is a wonderful collection of plants, most of them characteristic of our own chalk and limestone, but including several southern species such as *Lactuca perennis* and *Sisymbrium austriacum*.

On Sunday afternoon a walk was arranged in the charming Forêt de Soignes, with its varied soils and equally varied vegetation.

After the close of the meeting, a three days' excursion (May 23rd to 25th) was made. Genck in the "Campine," was first visited. This village lies in the midst of a sandy tract of flat country on the Dutch border, with much heath and inland dunes. In the depressions are shallow meres which are stocked with carp for a few years, then drained and oats sown on the mud left by the water. After two crops of oats have been taken off the depression is again flooded. The whole of this country is most interesting from the standpoint of its vegetation.

The second day was spent in the valley of the Hoegne, near Spa. The upper part of this valley is filled with fine woodland of oak and birch with an interesting ground-flora including *Polygonatum verticillatum* and *Trientalis europæa*. The stream rises in a great tract of upland moor about 2,000 feet in altitude, (the Haute Fagne, adjoining the "Hohe Venn" of the northern Eifel) bearing vegetation composed of *Eriophorum vaginatum*, *Scirpus cæspitosus* and *Sphagnum* as a ground-work, with *Vaccinium uliginosum*, *Vitis-Idæa* and *Oxycoccos*, *Andromeda*, *Arnica montana*, *Trientalis europæa*, *Maianthemum bifolium*, etc., etc. Later on the beautiful Hertogenwald round the artificial lake of Gileppe was visited.

On the third day a visit was paid to the locality, near the

German frontier, of the "zinc plants" *Viola lutea calaminaria*, *Alsine verna*, *Armeria elongata*, and *Thlaspi alpestre calaminare*. These occur in great abundance on the old spoil heaps of zinc mines, and at the period of the visit (May 25th) were all in flower together, presenting a most beautiful sight. *Asarum europæum* in one of its few Belgian localities was afterwards seen.

From these very brief notes some idea will be gained of the varied interest of the excursions, the arrangements for which were both simple and practical, so that no hitches of any kind occurred. They were all organised by M. Massart, who accompanied the party on every occasion, and was often assisted by other botanists with special local knowledge. M. Massart's wide and thorough knowledge of Belgian vegetation, his indefatigable zeal in satisfying the visitors' thirst for information, and his very great personal kindness and charm, combined to make him an ideal guide, and to render the excursions as enjoyable and instructive as they could possibly be. A short programme giving the essential features of the excursions and a number of outline maps, diagrams and sections illustrating the climate, geology, soil-relations and vegetation of the districts visited added greatly to the ease with which the features were understood. Mention should also be made of M. Massart's magnificent " Esquisse de la Vegetation de la Belgique" in two volumes, one of text and one containing a beautiful series of photographs, a copy of which was presented to every member of the Congress. The thoroughness with which the climate, geology and soils of Belgium have been studied greatly assists the student of its vegetation.

REVIEW.

" Fossil Plants." A Text-book for Students of Botany and Geology. By A. C. Seward, F.R.S. Vol. II with 265 Illustrations. Cambridge, at the University Press, 1910. Pp. XXII. and 624. Price 15/-

We have waited a long time for the second volume of Professor Seward's book, Vol. I of which appeared in 1898. The author says in his preface: " Had Volume II been written ten years ago, the discoveries made in the course of the last decade would have given an out-of-date character to much of the subject-matter." This is true; fossil botany, just at present, is a subject in which books soon get superannuated. Still, we are glad to be assured that the author will not act on the same Fabian principle in the preparation of Vol. III which will be devoted to the Seed-plants.

The present volume is chiefly occupied with the Lycopods and the Fern-like plants. The first chapter, however, (chap. XII of the whole book) completes the account of the Sphenophyllales, begun in Vol. I, by the description of *Cheirostrobus* and other types of fructification, more or less recently discovered. The question of the nature of the sporangiophore is shortly referred to, the author pointing out that if the leaf is in phylogenetic origin a " branch-system of a primitive undifferentiated sporangium-bearing thallus" (Tansley); our faith in the importance of such morphological discussions is shaken (p. 16). The question whether the differentiation of the sporangiophore was prior or subsequent to that of the leaf is, however, one which may still reasonably appeal to the morphologically inclined.

In the short chapter on Psilotales (wisely treated as a distinct group) we are told that " it is doubtful whether any useful purpose is served by retaining the genus *Psilophyton*" (p. 29). This may come as a shock to the geological reader, but the botanist will welcome the extinction of a myth.

The 250 pages devoted to the Lycopods begin, according to the author's custom, with a sketch of recent forms, illustrated by some characteristic figures of habit and structure, which will be a great help to the non-botanical student. The fossils start with the Isoëtaceæ and *Pleuromeia*, a curious Triassic genus which has been regarded as connecting the Lepidodendreæ with *Isoëtes*. The author appears to accept the statement that the sporangium in *Pleuromeia* is on the lower side of the sporophyll, a character which scarcely seems consistent with Lycopod affinities.

Next comes an account of the herbaceous fossil Lycopods, our knowledge of which has increased a good deal in a short time. It is curious that there is no known case of homospory among these plants, unless it be in the Mesozoic *Naiadita*.

Chapter XV. ("Arborescent Lycopodiales") includes the genus *Lepidodendron*, in the widest sense, *Lepidophloios* being treated as a sub-genus.

The anatomy of the stem is described in detail in *Lepidodendron vasculare*, Binney (*L. selaginoides*, Carruthers). The difficulty that the cells of the cambium and those of the secondary wood do not usually fit on to each other is pointed out; this fact probably indicates that growth had ceased naturally some time before death.

In the section on *Ulodendron* and *Halonia* the author inclines to Mr. Watson's view that the ulodendroid scar marks the insertion of a deciduous branch and not of a cone, a view confirmed by Renier's recent work. He is also sceptical as to the cone theory in the case of *Halonia*, chiefly on the ground of the difference in stelar structure between the tubercle and the axis of the cone. Neither does he believe that the distinction between *Halonia* and *Ulodendron* is of generic value.

Throughout the account of the anatomy of *Lepidodendron* Professor Seward adheres to his term "secretory zone" for the layer corresponding in position to the phloem. His scepticism as to the presence of true phloem in these plants serves, at any rate, to call attention to points in the anatomy which need fuller investigation.

In accordance with his view of *Ulodendron*, the author discredits the idea of sessile cones, and believes that all cones were borne terminally on slender shoots, as is known to have been the case in some forms.

The value of Maslen's work on *Lepidostrobus* is fully recognised; in discussing *Spencerites*, the author attaches importance to Lang's comparison between this type of fossil cone and the recent *Lycopodium cernuum*, a point on which some difference of opinion prevails.

In the chapter on *Sigillaria* an interesting sketch of the old controversy between Williamson and the French school is given in a few words. The victory rested with Williamson who successfully maintained the cryptogamic nature of the genus and its close affinity with *Lepidodendron*. Our knowledge of the internal structure of *Sigillaria* has grown rapidly of late years, owing to the work of Bertrand, Kidston, and Arber and Thomas. Professor Seward publishes, for the first time, figures of the anatomy of *S. elongata* described by Bertrand in 1899.

In chapter XVII. the somewhat difficult subject of the rhizomes and roots of fossil Lycopods is dealt with. The author points out that the evidence for the connection between *Stigmaria* and the *Lepidodendron* stem is "still very meagre" (p. 233). He inclines to accept the views of Grand 'Eury as to the development of the aerial shoots of *Sigillaria* from pre-existing rhizomes of the Stigmarian type; the evidence, however, seems to be still somewhat vague and unsatisfactory. An excellent account of the anatomy of *Stigmaria* and its rootlets is given; our knowledge of the latter has received an interesting addition in Professor Weiss's discovery of a vascular connection between the central strand and the cortex.

The Bothrodendreæ have a chapter to themselves; in this ancient group of Lycopods, going back to the Devonian, the anatomical characters, recently determined by Mr. Lomax, are like those of a *Lepidodendron*, while the superficial features rather suggest the smooth-barked Sigillarias. The cones afford no certain criterion, for Mr. Watson's *Bothrostrobus* somewhat resembles the strobilus of a recent *Selaginella*, while Zeiller's *Lepidostrobus Olryi*, identified by Mr. Kidston with the cone of *Bothrodendron minutifolium* is of the type of other Lepidostrobi, though on a small scale. We shall soon have a very complete knowledge of *Bothrodendron*, if Professor Weiss's identification of his *Stigmaria* with centripetal wood as belonging to this genus should be confirmed.

The last few pages of chapter XVIII are occupied with General Considerations on fossil Lycopodiales. The anatomical evolution of the group, in relation to the increasing dominance of the secondary wood, is traced, while the apparent absence of secondary phloem suggests to the author that "the physiological division of labour may have been less complete in the tissue-systems of the Palæozoic Lycopods than in the more highly specialized organs of such an extinct genus as *Lyginodendron* or than in recent plants" (p. 269).

The next chapter is concerned with *Lepidocarpon* and *Miadesmia* "seed-bearing plants closely allied to members of the Lycopodiales," which, as the author says, teach us that "certain Lycopodiaceous plants of the Palæozoic era had reached an important stage in the evolution of a seed" (p. 275). His further point—"the value of this discovery as an argument in favour of the view that some Gymnosperms are derived from Lycopod ancestors"—will not meet with such general acceptance.

The second half of the volume is devoted to Ferns and Fern-like plants and begins with a useful sketch of the recent Ferns, in which just those points that are of importance to the palæobotanist are selected for consideration. The author, while accepting current views as to the important position of the Pteridosperms in the Palæozoic Floras, rightly urges the need for a critical consideration of the facts. He speaks with some sarcasm of allowing the "ferns or fern-like plants the peculiar position of universal ancestors," but it must be remembered that there is no *à priori* improbability in all the seed-plants having had a common ancestry, but rather the reverse. That many of them were derived from the Ferns he would be the first to admit.

The following passage is both amusing and just:

"Like the earlier writers who described fossils as *lusus naturæ* fashioned by devilish agency to deceive too credulous man, the discovery of seed-bearing plants with the foliage of ferns threatened to disturb the mental balance of palæobotanists" (p. 282).

The first family of fossil Ferns to be described is that of the Osmundaceae, a group which has now come to be of the greatest interest, owing to the work of Kidston and Gwynne-Vaughan, who have succeeded in tracing back its history to the Permian or beyond. Their results are based on anatomical evidence, but the antiquity of the family is further confirmed by cases in which the sporangia are preserved. Its earliest members become merged in the synthetic group of Palæozoic Ferns called Primofilices by Mr. Arber and Coenopterideæ by Professor Seward. A fine section of the Permian Osmundaceous Fern *Thamnopteris Schlechtendalii* is depicted in the frontispiece to the present volume.

The geological history of the other Fern families is traced, so far as the available material permits. It is interesting to note that both in the Gleicheniaceæ and Matonineæ (the latter a considerable group in Mesozoic times) conclusive anatomical evidence is afforded by specimens from the Wealden of Belgium, preserved as lignite, which "might easily be mistaken for rather old and brown pieces of recent plants" (p. 353). A diagrammatic figure of a section of *Matonidium* from this remarkable material is given on p. 310 (Fig. 237, D). It is to be hoped that the specimens may eventually be described and figured in detail by the discoverer, Professor Bommer.

Leaving the Leptosporangiate families, now forming by far the chief part of the Ferns, we next come to the Marattiales, to which so important a rôle in the Palæozoic Flora has been attributed. Chapter XXII is limited to the evidence drawn from the fronds and sporangia, while the anatomical characters are discussed under the heading Psaronieæ, in the following chapter. It would perhaps have been the more logical course to include the latter under the general heading "Marattiales," for the anatomical evidence from the *Psaronius* stems is now the best proof we have of the existence of Marattiales in Palæozoic tissues. Of course the proof is far from absolute; as the author says: "it is not impossible that *Psaronius* stems bore fronds which produced Pteridosperm organs of reproduction" (p. 426). As the sporangial characters are certainly not conclusive, it will be seen that the position of the family in the primary floras is precarious.

Chapter XXV is headed Cœnopterideæ. This new name is used by the author in two somewhat different senses; on p. 365 it is proposed as a synonym for Botryopterideæ, while on p. 433 it is employed in a wider sense, corresponding to Arber's Primofilices, of which the Botryopterideæ are only a part, though the most important. In the former sense the name is superfluous; in the latter its introduction is justified. In spite, however, of Professor Seward's well-founded criticism of the word Primofilices, as implying the primitive or primary nature of the group, Mr. Arber's name is so clear and intelligible that it is not likely to go out of use. The new designation, Cœnopterideæ, refers to the *generalized* character of these early Ferns.[1]

The author adopts the division of Botryopterideæ into two families, the Botryoptereæ and the Zygoptereæ; in the former he includes *Tubicaulis* on account of its simple stelar structure, while *Stauropteris* is placed under Zygoptereæ. In the latter point he follows Dr. Paul Bertrand, from whom he differs as to the position to be assigned to *Tubicaulis*. P. Bertrand's reference of Williamson's *Zygopteris Grayi* to *Ankyropteris*, which the author provisionally adopts, is incorrect, if, as Mr. Kidston finds, its petiole is identical with *Z. di-upsilon*, for the latter is a typical *Etapteris* on the Bertrand classification.

Kidston and Gwynne-Vaughan, whose important work on Fossil Osmundaceæ has been already mentioned, said that if (as they believe) the Zygopteroid line of descent is near that of the

[1] *κοινός*=Lat. *communis*, common or general.

Osmundaceæ, we must be prepared for the existence of a *Zygopteris* with a solid xylem like that of *Thamnopteris*: "such a discovery, in fact, we hopefully anticipate." This prediction has now been fulfilled by Mr. Gordon's discovery of the stem of *Diplolabis*, a genus closely allied to *Zygopteris* (p. 448).

Professor Seward concludes the chapter as follows: "The conclusion arrived at is that while the Cœnopterideæ foreshadow in some of their characters more than one group of more recent Ferns, some at least of their members afford convincing evidence of the correctness of the view—which is also that of Dr. Kidston and Mr. Gwynne-Vaughan—that the Osmundaceæ and the Cœnopterideæ are offshoots of a common stock" (p. 472).

As regards the Hydropterideæ, Nathorst's discovery of sporocarp-like bodies in association with the Rhætic *Sagenopteris*, strengthens the belief that this genus may really, as the form of the frond suggests, belong to the Marsiliaceæ; otherwise there is no trustworthy evidence of pre-Tertiary Water-ferns.

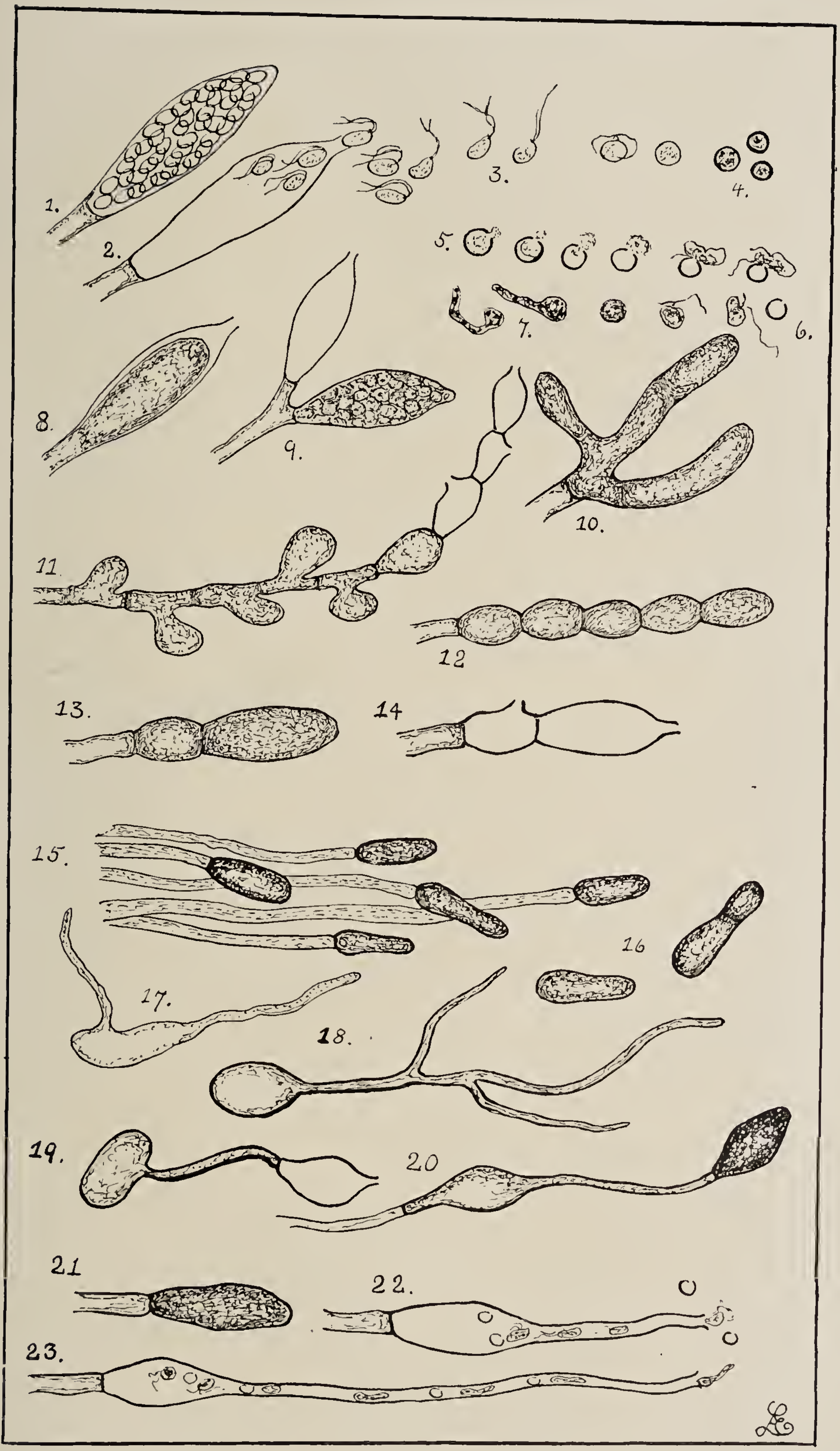
Chapter XXVII, the last in the volume, is headed "Genera of Pteridosperms, Ferns and *Plantæ incertæ sedis*." "Some of the genera, the smaller number, are no doubt true Ferns"; most of them are in all probability Pteridosperms or Cycadophytes. This chapter is intended to clear the ground, "in order that the Chapter in Vol. III devoted to this important group may be limited to more completely known types" (p. 484). Among the more or less doubtful genera dealt with is *Glossopteris*, "a characteristic member of a Permo-carboniferous flora which flourished over an enormous area"—India, S. Africa, Australia, and S. America. The interpretation of the characters of the rhizome (*Vertebraria*) is still quite uncertain, but if *Blechnoxylon*, with its zone of what appears to be secondary wood, is rightly referred to *Glossopteris*, we have a possible indication of Pteridospermous affinities. Otherwise the sporangia observed by Mr. Arber in association with the scale-leaves of *G. Brownii* are the chief point of botanical interest, in a group which has hitherto chiefly appealed to the geographer and the stratigraphical geologist. It is a suggestive fact that the scale-leaves of the allied *Gangamopteris* have been found associated with Gymnospermous seeds.

In looking through the long list of frond-genera described in this chapter, it is curious to see in how few cases there is any good evidence of their belonging to Ferns; either there is no evidence at all, or it is on the side of spermophytic affinities. It is interesting to find among the Mesozoic fossils a number of doubtful genera, which may well have been belated Pteridosperms, or perhaps Cycadophytes of unknown families. A promising field for research here remains to be explored.

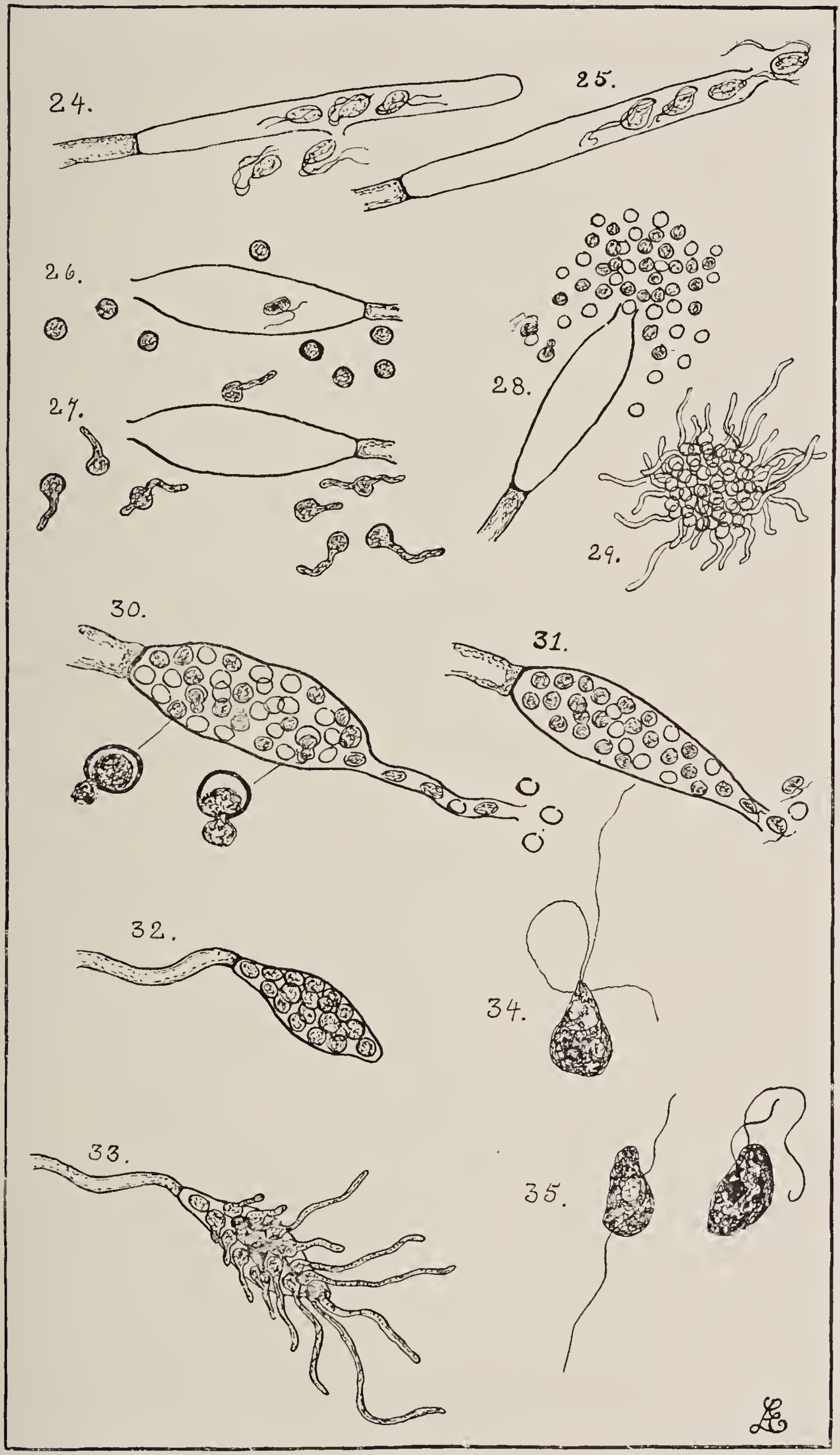
The volume as a whole is a perfect mine of information, brought thoroughly up-to-date, and sifted with the sound judgment which is characteristic of the author. It is beyond comparison the best text-book for the groups to which it relates, and will of course be indispensable to botanists. The numerous illustrations are of the greatest service to the reader, and in view of their abundance, we cannot complain if, in a few cases, they are more diagrammatic than we might have wished.

We shall look forward with great interest to the appearance of Vol. III, in which some questions of very deep importance to the student of evolution will come up for discussion. D.H.S.

THE NEW PHYTOLOGIST. VOL. IX., PLATE I.



LECHMERE—*SAPROLEGNIA.*



LECHMERE—*SAPROLEGNIA.*

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THE INTER-RELATIONSHIPS OF THE BRYOPHYTA,

By F. CAVERS, D.Sc.

[FIGS. 44—54.]

IV. ACROGYNOUS JUNGERMANNIALES.

IN the Acrogynæ, the plant-body, or at any rate the portion of it which bears the sexual organs, is differentiated into stem and leaves. In some genera there is a thalloid (*Pteropsiella*, *Metzgeriopsis*) or even filamentous (*Protocephalozia*) phase in the life history of the sexual generation, but even in these cases the sexual organs are borne on leafy shoots. When archegonia are produced, whether on the main axis or on its branches, the apical cell itself is transformed into an archegonium, and the vegetative growth of the axis or branch is terminated. The leaves are developed in spiral succession from a three-sided (rarely two-sided) apical cell, and are arranged in two lateral rows, in addition to which there is often a ventral row of under-leaves, or amphigastria, frequently differing from the lateral ones in size and shape.

The antheridia are borne in the axils of more or less modified leaves—" male bracts " or " perigonial leaves." The archegonia are usually surrounded by a special sheath, the " perianth," which arises as a ring-like outgrowth, when the archegonia are ripe, from the tissue immediately outside the group of archegonia; there is frequently, immediately outside the perianth, an " involucre " consisting of more or less modified leaves (" female bracts "). The antheridium is usually spherical, with a slender stalk; the archegonium-neck consists of five rows of cells. The sporogonium is always differentiated into seta and capsule. The capsule opens by four valves, and elaters are always associated with the spores.

The vast majority of the genera and species of Hepaticæ belong to this great group, which has a world-wide distribution but is especially developed in the wet forest regions of the tropics. In round numbers, the Acrogynæ include all save some 60 genera and 700 species of the 250 genera and 4,500 species of Hepaticæ which have been described up to the present time. In Britain, there are only some 70 genera and 250 species of Hepaticæ, and of these 50 genera and 200 species belong to the Acrogynæ. These figures show the striking preponderance of the Acrogynæ over the rest of the Hepaticæ ; and the poverty in species of the Hepatic flora of Britain, which resembles the North Temperate regions generally in this respect, is shown by the fact that there are several Acrogynous genera with more species than the total number of British Hepaticæ, e.g. *Plagiochila* with over 500 species, *Frullania* with about 350, *Bazzania* with upwards of 300.

Before dealing with the classification and inter-relationships of the Acrogynæ, we may consider the chief morphological characters of the group, with special reference to the wealth of parallel developments which is one of its most striking features.

The size of the plant varies considerably in the Acrogynæ. Some of the epiphytic Lejeuneas, which grow on living leaves of ferns and flowering-plants, are only a few millimetres long and consist of delicate thin-walled cells, while some of the large bark-inhabiting forms of the same group (e.g. *Bryopteris*) reach a length of several feet and are firm and hard in texture. In his travels on the Amazon, Spruce found remarkable pendent festoons of epiphytic Frullanias, which often formed an important feature in the vegetation of wet tropical forests and which were too thick for a man's arms to surround them.

In the Acroygnæ, the apical cell of the shoot (Fig. 44) has almost invariably the form of a three-sided pyramid, from which three sets of segments are cut off. One side of the apical cell is parallel with the ventral surface of the stem, and the other two sides meet in the middle line above, hence one set of segments is ventral and the other two sets dorso-lateral. From each of the latter a leaf is formed, while the ventral segment may or may not produce an underleaf (amphigastrium). The form of the apical cell is directly related to the size of the underleaf as compared with the lateral leaves. Where the underleaves are well-developed, the three sets of segments are about equal in size, and the apical cell forms in surface view an equilateral triangle; where no underleaves are formed, the ventral segments are narrow, the apical cell appearing in surface view as an isosceles triangle with a narrow base. In the thalloid vegetative portion of the plant-body in *Metzgeriopsis*, and in the leafy shoot of *Pleurozia* and *Arachniopsis*, however, the apical cell is two-sided, and there are of course only two (lateral) sets of segments.

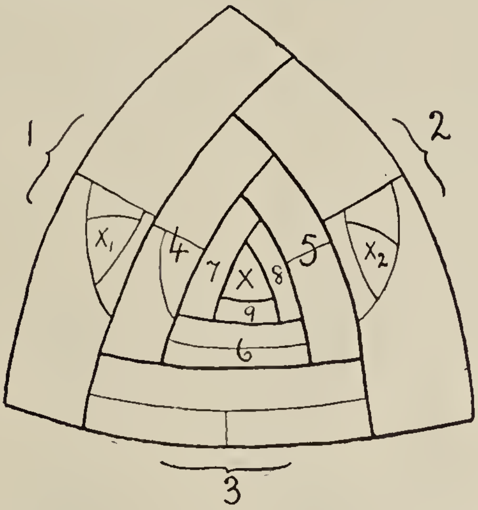


Fig. 44. Diagram of the apical growing-point, seen from the front. X, is the apical cell of the main axis; the last nine segments cut from it are numbered; X_1, X_2, are the apical cells of branches.

Each lateral segment of the apical cell divides first by a radial wall into an upper and a lower cell. This wall may be nearer either the upper or the lower side of the segment, and from the larger of the two cells an inner cell is next cut off which contributes to the formation of the stem, while the two outer cells (upper and lower) give rise to the young leaf. Even when the mature leaf shows no trace of lobing, the very young leaf is distinctly two-lobed, each lobe bearing a mucilage-papilla. In fact, the ultimate form of the leaf depends on the further development of the originally similar and separate upper and lower lobes of the very young leaf. In species with entire leaves, the two lobes grow together (*i.e.* are carried up by common growth at the base) from the first; whereas in forms with divided leaves the lobes grow out independently for a shorter or longer time. The growth of the leaf is at first apical, segments being cut from the terminal cells by transverse walls. When *only* transverse divisions occur in the two primary cells, we get a leaf consisting of two diverging rows of cells (*Arachniopsis*). From these considerations, it is easy to account for the extraordinary variety in form of the mature leaf which is met among the Acrogynæ and which contrasts strongly with the remarkable uniformity of the Moss leaf—the leaves of Mosses are never lobed, though the margin may be slightly toothed. The leaves are at first inserted transversely on the stem, and the insertion remains as a transverse line when the leaf consists of two or more simple cell-rows (*Arachniopsis*, *Blepharostoma*), but as a rule the insertion line becomes shifted so that it runs obliquely across the stem. This shifting is due to unequal growth in length of the upper and lower portions of the stem tissue. If this growth is *hypotropic* (greater on the lower side), the stem curves upwards, away from the substratum, at the growing tip of the shoot, the line of insertion

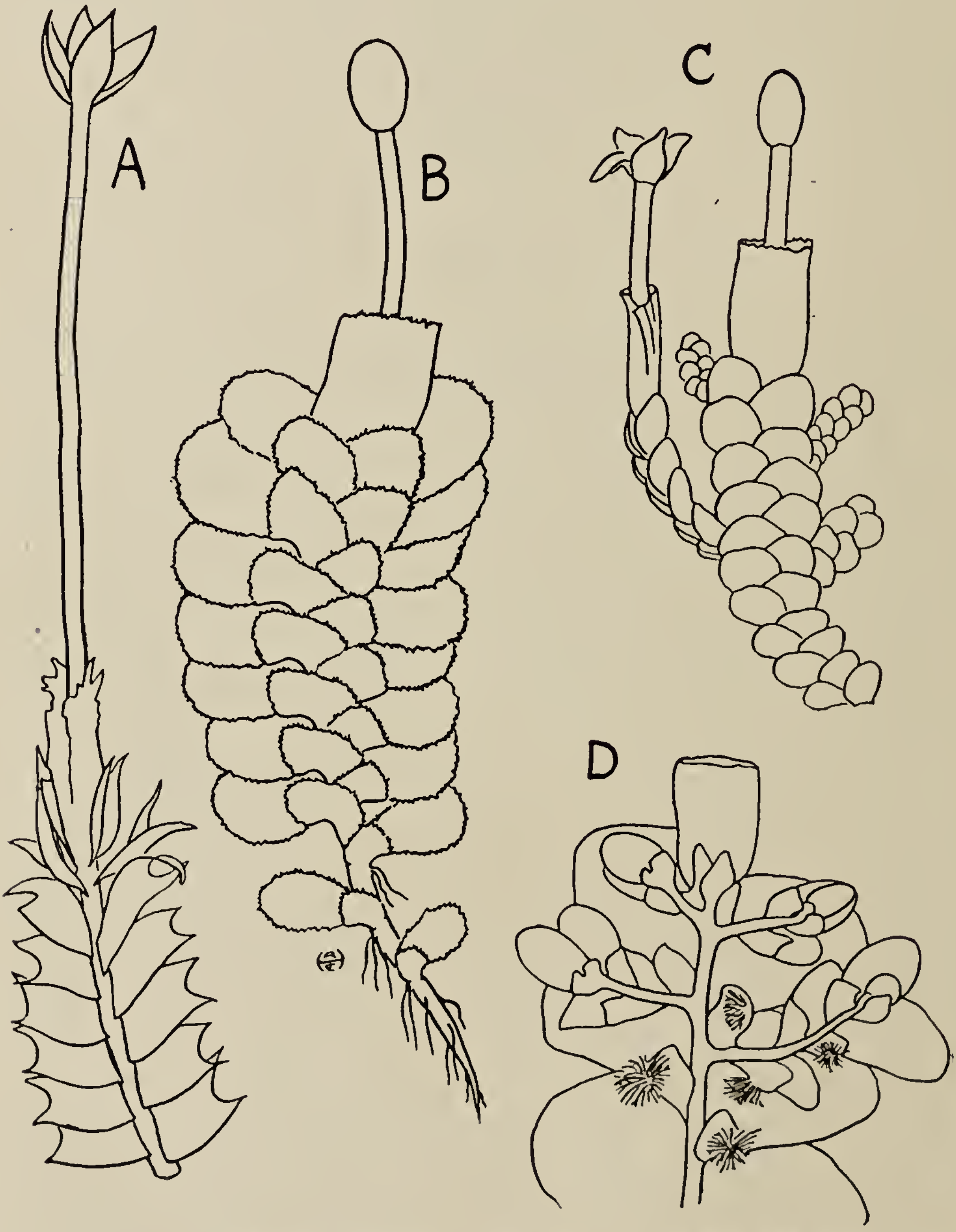


Fig. 45. A, *Lophocolea bidentata*, dorsal view; B, *Scapania nemorosa*, dorsal view; C, *Radula complanata*, dorsal view; D, *Radula*, ventral view. Descriptions of leaf-insertion, leaf-lobing, and perianth are given in the text.

runs forwards and downwards, and the fore edge of the leaf is overlapped by the hinder edge of the next leaf in front—this is the *succubous* arrangement (Fig. 45, A. B). If the growth of the stem is *epitropic* (greater on the upper side), we get the reverse or *incubous* arrangement (Fig. 45, C; Fig. 46).

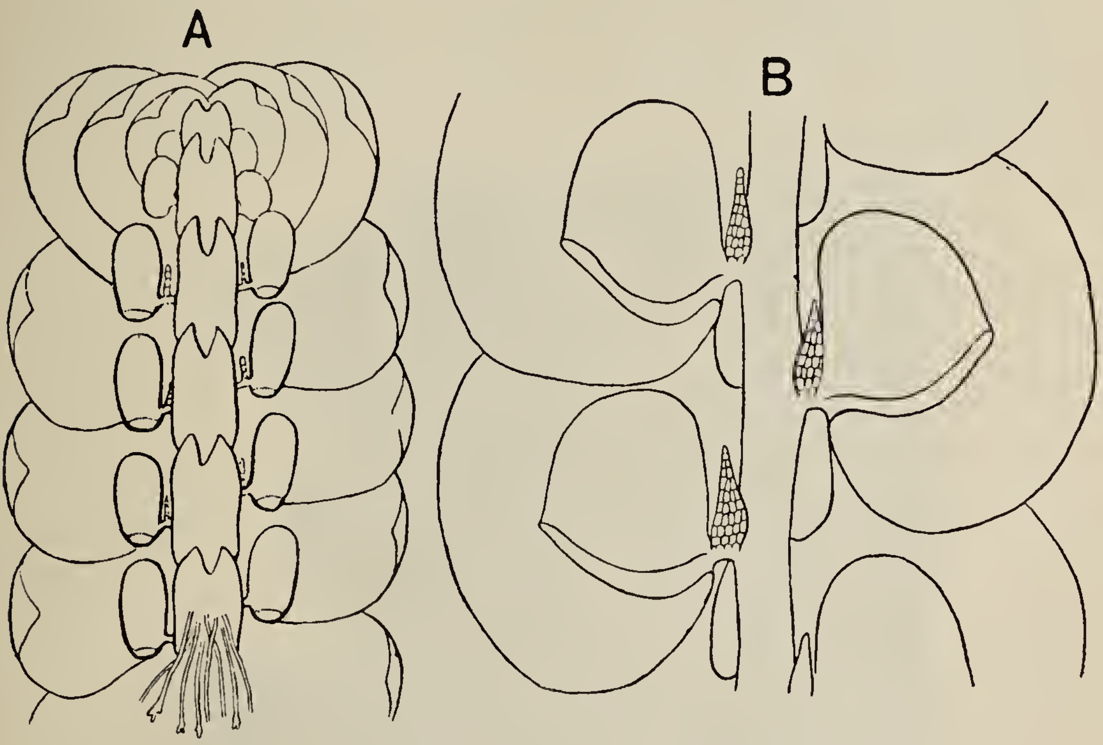


Fig. 46. Leaf-pitchers of *Frullania*, as seen on ventral side of the shoot of (A) *F. tamarisci* and (B) *F. dilatata*.

Taking first the forms in which the leaf is flattened in one plane, the insertion being a straight or slightly curved line, we find every transition between leaves which are entire or very slightly notched and those which are divided to the base into two or more lobes. With this type of insertion, which may be either succubous or incubous, the lobes in the case of notched or divided leaves are usually equal in size. The form of the leaf is, however, often complicated when the lobing is accompanied by folding, each lobe being attached independently to the stem and the two lines of attachment meeting at an angle which is often very sharp, while the leaf itself shows a more or less acute fold or keel. In these "complicate-bilobed" leaves the lobes may be about equal in size (e.g., *Marsupella*, some species of *Scapania*) and the leaf is neither incubous nor succubous. But in most cases the lobes of the complicate leaf are unequal in size, the dorsal lobe being the larger as a rule and the leaf arrangement incubous (e.g., *Radula*, *Porella*, *Frullania*), though sometimes the ventral lobe is the larger and the leaves succubous (*Diplophyllum*, most species of *Scapania*). In some cases, the leaves are "fused" in pairs across the dorsal side of the stem (*e.g.*, some species of *Calypogeia*); in others, the leaves are not only united dorsally but their lower margins are continuous with the sides of the underleaf that stands between each pair of leaves (*Arnellia*, *Southbya*); while in *Syzygiella*, which has no underleaves, the leaves are joined both above and below, so that the stem appears to pass through a series of funnel-like double leaves.

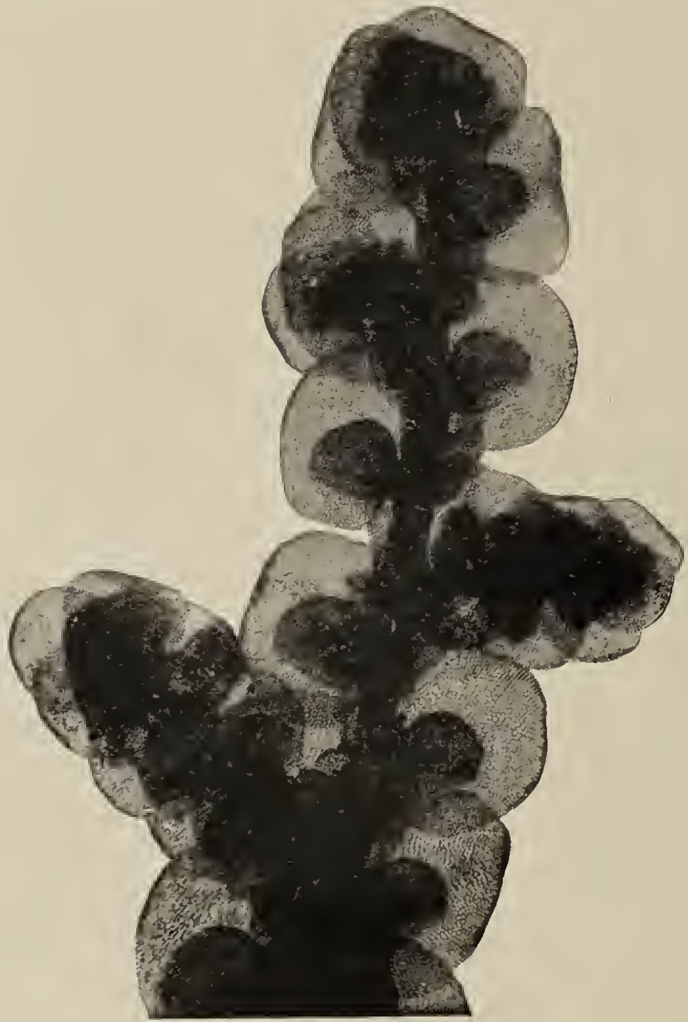


Fig. 47. *Frullania dilatata.*

It is among the forms with folded leaves that we find some of the most remarkable examples of the plasticity of the Acrogynous leaf, mostly serving for the storage of water in various ways. In *Mytilopsis*, the leaf is so sharply folded that the two lobes lie almost parallel, like the valves of a mussel shell open anteriorly by a narrow slit, while the sharp keel bears a narrow wing. In *Micropterygium*, *Gottschea*, etc., the leaf bears a conspicuous wing similar to that found in the Moss-genus *Fissidens*—in *G. ciliata* there are two wings and the leaf is H-shaped in cross-section. In several genera, belonging to different families, we find *paraphylls*—leaf-like or filamentous outgrowths arising from the stem between, and in addition to, the ordinary leaves; in the curious genus *Stephaniella*, the leaves soon lose their chlorophyll and then serve as transparent scales covering the dense mantle of green filamentous paraphylls with which the stem is clad. Perhaps the most beautiful of these modifications, however, are the *water-sacs* or pitchers, formed by the infolding of either the entire leaf, or the large upper lobe, or, more commonly, the small ventral lobe. Sometimes the pitchers are provided with a valve or trap-door like that of the Bladderwort pitcher. The small ventral-lobe pitchers of *Frullania* (Figs. 46, 47) are well known, but similar pitchers occur in various genera belonging to different families, and in *Polyotus* (Fig. 48) we get a profusion of pitchers developed not only on the side-leaves but also on the underleaves.

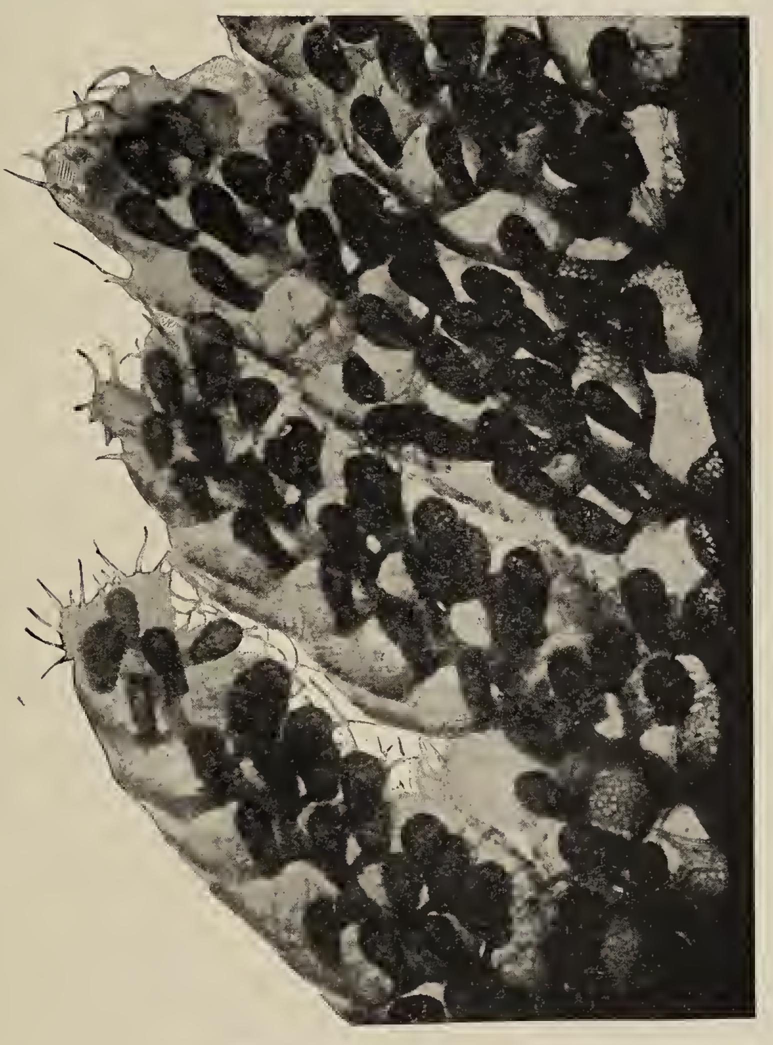


Fig. 48. *Polyotus magellanicus.* Part of a plant showing lower surface of four of the ultimate branches, with numerous water-sacs.

Each of the ventral segments cut from the apical cell divides first by a tangential wall; the inner cell adds to the stem tissue, the further development of the outer cell varies considerably. In the simplest case (e.g., *Lejeunea calcarea*) each of these outer cells simply gives rise to a single row of cells on the underside of the stem, but as a rule a radial division occurs giving two cells placed side by side, then each of these produces a mucilage papilla, and an underleaf is formed. The underleaves show hardly any of the modifications exhibited by the side-leaves, as might be expected from their different position. The side-leaves are turned towards the light, the underleaves are usually appressed to the substratum and cut off from light, hence they are usually smaller and often absent altogether. Frequently, however, the shoot grows more or less erect and the underleaves may be equal in size to the side-leaves, the shoot showing practically radial symmetry.

In striking contrast to the varied external morphology of the shoot in the Acrogynæ, we find practically an entire absence of histological differentiation in the stem and leaves. The tissue of the stem is generally quite uniform; though the inner cells may have thinner walls than the outer cells, we rarely find anything approaching even the simple type of conducting strand found in so many Mosses, much less the elaborate differentiation seen in the Polytrichaceæ, etc. In some of the Lejeuneas and Frullanias. certain cells of the leaf are much larger than the others, these "ocelli" being either scattered or arranged in a median line running up the leaf. In a few forms (e.g., *Herberta*, *Diplophyllum*) there is a "midrib" consisting of a band of elongated cells, which as shown by Tansley (83) serve for conduction. The leaf is rarely more than one cell thick, though in some cases (species of *Gottschea*, etc.) it is several-layered at the base and for some distance upwards. The rhizoids are typically unicellular and unbranched, or slightly branched at the ends, though Goebel (33) notes in *Gottschea* the occurrence of numerous septa in the distal branched portion of the rhizoids.

Various features of interest in the vegetative organs of the Acrogynæ are described by Goebel (32). For an account of asexual reproduction as exhibited in this group, reference may be made to a paper published in this Journal (5).

The distribution of the sexual organs varies greatly, but the commonest condition is that in which the antheridia and archegonia are borne on the same plant but in separate groups or "flowers."

The antheridia (Fig. 52, B, C), which are spherical or ovoid with a slender stalk, are borne in the axils of more or less modified "male bracts" (perigonial leaves), either singly or in groups of from two to about twelve; they are sometimes (*Scapania*, etc.) accompanied by filamentous or narrow leaf-like paraphyses. The perigonial leaves are always simple and symmetrical in form, even in species where the ordinary leaves are deeply divided into lobes differing greatly in size and shape and show other modifications (water-sacs, etc.). The antheridia are seldom borne in the axils of the underleaves where these are present, and they are often produced on special short catkin-like branches, the "male bracts" being crowded and often having saccate bases for the better protection of, and especially the retention of moisture about, the antheridia.

The archegonia are borne in terminal groups at the apex of the main axis, or of its ordinary branches, or of special short branches —the latter often arising from the underside of the stem. In any case, the development of an archegonial group—probably that of the first archegonium in the group—uses up the apical cell and thus terminates the growth of the stem. In the Lejeuneas a single archegonium is developed, and in *Frullania* (Fig. 52, D, E) only two or three, but in most cases the group contains a large number (sometimes a hundred or more) though as a rule a single mature sporogonium is produced. The archegonial group is surrounded by an "involucre" or "perichætium" consisting of leaves which usually differ in their larger size and in other respects from the ordinary vegetative leaves. The archegonial branch generally tends to grow erect, and the underleaves ("bracteoles") of the "involucre" are then nearly or quite as large as the leaves ("bracts") and are usually present even in species which lack underleaves on the rest of the shoot. The bracts are often more extensively laciniated and fringed than the vegetative leaves, as an adaptation for retaining moisture by capillarity, but on the whole they are, throughout the Acrogynæ, less specialised than the leaves. For instance, they are usually divided symmetrically by a median notch of greater or less depth, alike in species with entire rounded leaves and in those with the leaves cleft into a larger and a smaller lobe, and they never show special structures like water-sacs.

In the great majority of Acrogynæ, the archegonial group becomes surrounded by a tubular organ—the "perianth"—which arises within the involucre, making its appearance after the development of the archegonia themselves. As a rule, the formation of this organ occurs independently of fertilisation, though it probably does not reach mature size if no archegonia have been fertilised. The perianth is by most writers regarded as a structure formed by the fusion of the uppermost leaves (two or three in number according to the species) of the female axis. In many cases, the form of the mature perianth certainly supports the view that it corresponds to concrescent leaves, the orientation of which agrees with that of the ordinary vegetative leaves of the species. The union of two leaves and an underleaf, all remaining flat, gives a perianth of the "epigonanthous" type, having the form of a triangular prism, three angles or keels being formed by the united margins of the leaves; one of the flat sides is ventral, one of the keels dorsal—e.g., *Lophocolea* (Fig. 49, A). A modification of this is seen when no under-leaf takes part in the formation of the perianth—the latter is compressed laterally—e.g., *Plagiochila* (Fig. 49, B). When the perianth-forming leaves are folded, instead of being flat, we may again get a triangular perianth, but this time the third keel is ventral instead of dorsal; this "hypogonanthous" type (Fig. 49, C) occurs in many genera, e.g., *Cephalozia*, *Bazzania*, *Lepidozia*, *Porella*, *Frullania*, and the Lejeuneas. When no under-leaf enters into this type of perianth, we again have a compressed structure, but this time (Fig. 49, D) the flattening is dorsiventral—parallel with the substratum instead of at right angles to it (e.g., *Scapania*, *Radula*). But in many species the form of the perianth does not fall into line with these types, and if we support the interpretation that the perianth is invariably a foliar structure, it is not easy to account for the many cases in which it is devoid entirely of angles or keels; in other cases the interpretation is made difficult by the presence of additional keels, which may be without any definite orientation. According to Leitgeb (54) the perianth arises from the last segments cut from the apical cell before the latter becomes used up in the

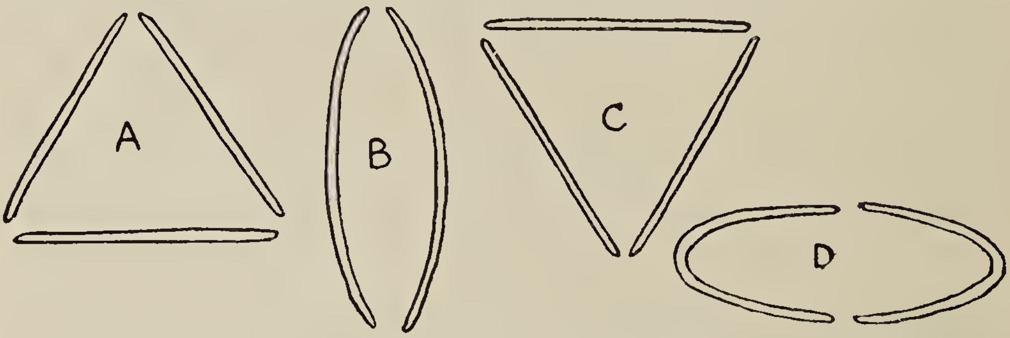


Fig. 49. Diagrammatic transverse sections of four types of perianth in Acrogynæ. A, is epigonanthous; C, hypogonanthous; B, compressed laterally; D, compressed dorso-ventrally.

formation of the archegonia. We have seen that vegetative leaves may undergo concrescence, and in some cases this occurs with the leaves (bracts) of the involucre. The perianth may be absent altogether—a condition especially found in species having a fruit-sac or marsupium.

In its fully-developed form, the marsupium is a tubular structure which grows downwards into the substratum, bearing rhizoids on its outer surface, while the young sporogonium develops inside it at the closed lower end, and the ripe capsule is thrust out of its open upper end when the seta elongates. The development of the marsupium has been investigated by Gottsche (34, 35) and by Leitgeb (57), and more recently by Goebel (32, 33) and by Douin (7). All the species possessing this remarkable structure were until recently classed together as an independent family, the "Geocalyceæ," but this is an entirely artificial group, the marsupial genera and species being scattered over four of the eight families of Acrogynæ now generally recognised. The independent origin of the marsupium in unrelated genera, and in certain species of otherwise normal genera, forms one of the most striking examples of homoplasy to be found even in the Hepaticæ. Moreover, the marsupium has clearly arisen in several different ways in different cases, as we shall presently see.

The whole subject of the arrangements for the protection and nutrition of the developing sporogonium has never received the detailed consideration which it deserves, though these arrangements appear to be of great importance in connexion with the phylogeny of the Acrogynæ. In the simplest case, typical of the majority of the Acrogynous genera, the young sporogonium is invested by (1) the calyptra formed from the venter of the fertilised archegonium, (2) the perianth, which arises as a ring-like outgrowth around the archegonial group, and which is doubtfully regarded as a concrescent leaf structure, and (3) the involucre of more or less modified leaves—all these envelopes being free from each other, while the foot, or enlarged base of the sporogonial seta, is embedded in the base of the calyptra (Fig. 50, I.).

The writer has investigated the morphology of the sporogonial envelopes in species belonging to the majority of the genera of Acrogynæ, and has found that in nearly half of the genera (excluding the Lejeuneaceæ), there are indications of stages leading up to the fully developed marsupium of the "Geocalyceæ." Starting from the simplest condition in which the three envelopes—calyptra,

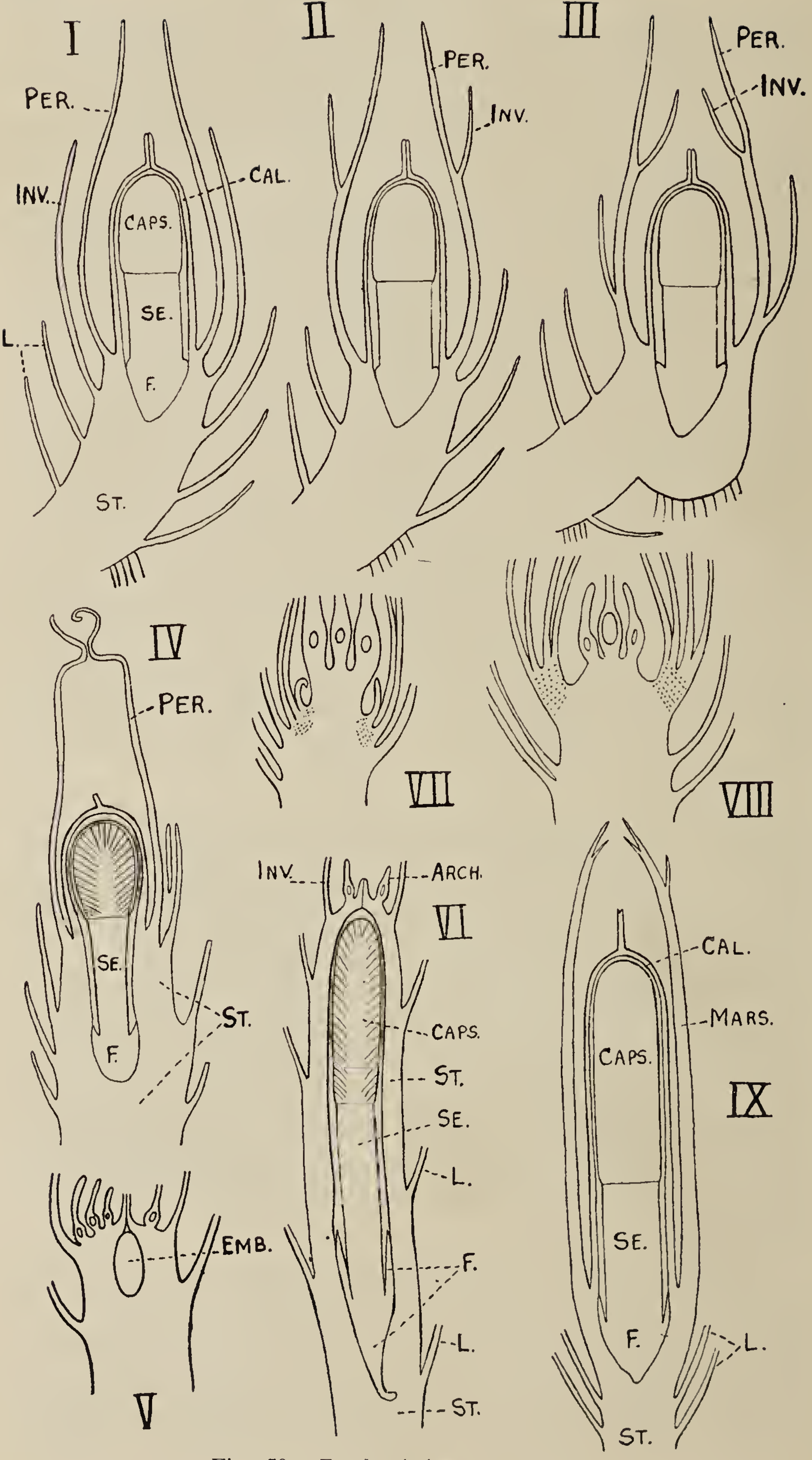


Fig. 50.—*For description see next page.*

Fig. 50. Diagrammatic longitudinal sections of various Acrogynæ, showing the archegonial group and the sporogonium with the structures developed around them. I.—Perianth and involucre free (e.g., *Lophocolea*, *Plagiochila*, *Frullania*). II.—Perianth and involucre "fused"—*i.e.*, carried up by the growth of a basal ring-like zone of stem tissue (e.g., *Eucalyx*). III.—Perianth and involucre "fused"; the formation of an incipient marsupium ("fruit-sac") indicated by the bulbous swelling of the stem below the foot of the sporogonium (e.g., *Nardia geoscypha*) IV.—The seta and foot of the sporogonium have penetrated for some depth into the stem tissue (e.g., *Cephalozia bicuspidata*). V. and VI.—Two stages in the development of "cœlocauly"—the complete embedding of the sporogonium in the stem tissue e.g., *Gottschea*, *Trichocolea*). VII. to IX.—Three stages in the development of the erect marsupium of *Isotachis*. Arch., archegonia; cal., calyptra; caps., capsule; emb., embryo sporophyte; f., foot; inv., involucre; l., leaf; mars., marsupium; per., perianth; se., seta; st., stem. Figures IV. to IX. are from Goebel.

perianth, involucre—are free from each other and the sporogonium foot extends only to about the insertion of the involucre, we may trace various lines of specialisation, resulting in the more complete investment of the young sporogonium, and culminating in the various types of fruit-sac which can be distinguished among the marsupial Acrogynæ.

Among the various processes which tend to facilitate the nursing of the young sporogonium, and of which several may take place hand in hand, the simplest is the following. The seta, capped by the absorbing foot or haustorium, grows actively downwards into the stem tissue, which may either remain unaltered or may grow in thickness so as to form a thick protective and food-storing sheath around it. In many cases, the foot penetrates below the insertion of the involucre, so that only the capsule and upper part of the seta of the ripe, but not yet exserted, sporogonium are covered by the calyptra, but no further special development occurs (Fig. 50, IV.). In other cases, however, the portion of stem underlying the archegonial group grows actively, in such a way that more and more of the lower portion of the sporogonium becomes sunken in it and surrounded by a thick sheath formed of stem tissue, while the calyptra gradually dwindles in size. In *Leiomitra*, the calyptra is still recognisable as a thin envelope covering the capsule itself. In the allied genera *Trichocolea* and *Polyotus*, there is no calyptra at all, if we limit the idea of a calyptra to the result of growth of the archegonium venter; the so-called "calyptra" is here in reality formed from the stem tissue, into which the lower end of the sporogonium burrows deeply, and which bears at the apex the unfertilised archegonia (and the neck of the fertilised one), while the involucral leaves are either carried up on its sides or form a crown at the top (Fig. 50, V., VI.). In the three genera just mentioned, there is no perianth, and the same is true of practically all the forms with a well-developed marsupium.

In a considerable number of genera, belonging to different families, we find a series of changes which lead up to the formation of a distinctly sac-like structure, arising after fertilisation from the tissue of the stem and resulting in the development of a definite and conspicuous marsupium. Three main types may be distinguished.

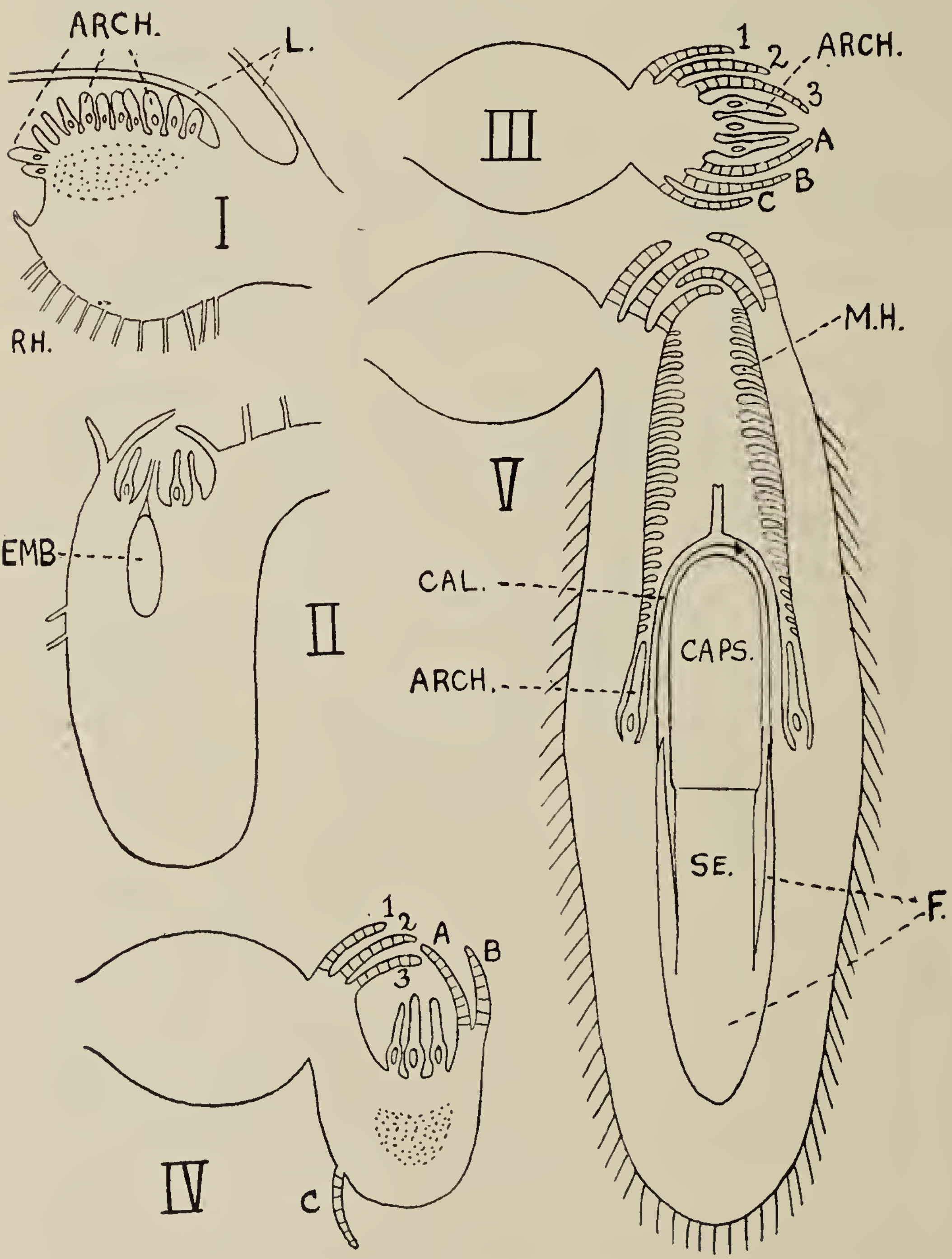


Fig. 51. Stages in the development of the solid marsupium of *Tylimanthus* (I., II.) and of the hollow marsupium of *Kantia trichomanis* (III. to V.) Lettering as in Fig. 44; rh., rhizoids. All except V. from Goebel.

(1) The *Isotachis* type, in which the symmetry of the shoot remains unchanged, and the sac-forming meristem arises as a ring-like outgrowth of the stem tissue around the archegonial group (Fig. 50, VII. to IX.). (2) The *Tylimanthus* type, in which the sac-forming meristem is at first a solid mass of tissue, which grows at right angles to the long axis of the stem itself, and which invests and is penetrated by the embryo (Fig. 51, I., II.). (3) The *Acrobolbus* type, in which the meristem arises as a *hollow* ventral outgrowth from the archegonial branch (Fig. 51, III. to V.).

The origin of the *Isotachis* type of marsupium, in which the latter forms a direct linear continuation of the archegonium-bearing axis, may be traced in certain species described by systematists as having the perianth and involucre "fused" or concrescent. The "fusion" is brought about by the growth of a ring-like zone of tissue at the base of the perianth and involucre, both of which are carried up on a collar or tube (Fig. 50, II.) This process reaches different stages in different genera, e.g., *Nardia*, *Marsupella*, *Southbya*, and is most striking in *Isotachis*. Here the archegonial branch grows erect, and the stem-tissue grows up to form a long thick envelope which carries up with it the involucral and neighbouring leaves, as shown by Goebel (33). We thus get in *Isotachis* what looks like a perianth and has usually been described as one, but is really a marsupium. In the marsupia of the *Tylimanthus* and *Acrobolbus* types, the solid or tubular tissue-zone which produces the marsupium grows downwards, making a right angle with the axis of the plant and usually becoming attached by rhizoids to the substratum, into which it may burrow to some depth.

The beginnings of these different types of marsupium may be traced among certain species of *Nardia*. The case of *N. geoscypha* is specially interesting. Here the plant may either grow erect or horizontally. In the former case, the cup-like outgrowth which after fertilisation carries up the perianth and involucre, as already described, grows upwards and the developing sporogonium is parallel with the axis of the plant. In creeping plants, however, the ventral tissue of the stem grows so as to form a solid mass below the archegonial group; this swelling projects below and bears rhizoids, and its tissue contains food for the nutrition of the developing sporogonium, the absorbing organ (foot) of which becomes buried in the swelling (Fig. 50, III.) Thus in this species we have the beginnings of both the *Isotachis* and the *Tylimanthus* types of marsupium. The ventral form of incipient marsupium is found also in some other species of *Nardia* and in *Notoscyphus*, *Gyrothyra*, *Prasanthus*, and a few other genera. In these forms a perianth is usually still present, but it disappears in *Prasanthus*, and it rarely occurs in the more fully developed marsupia—obviously because it is no longer required, the protection of the sporogonium being taken over by the marsupium itself. The highest development of the solid type of ventral marsupium is found in the genera *Tylimanthus*, *Marsupidium*, and *Marsupellopsis*.

In the *Acrobolbus* type, which includes the majority of the marsupial Acrogynæ, the marsupium is tubular from the beginning, as compared with the solid *Tylimanthus* type, but transitions occur between the two types. In the *Tylimanthus* type the archegonial group shows dorsiventral symmetry, the archegonia being developed only on the dorsal side of the stem, and the marsupium is formed by active growth of the underlying tissue. In the *Isotachis* type the archegonial group shows radial symmetry, the archegonia being produced all round the apex of the erect stem, and the marsupium arises as a ring-like outgrowth of the stem-tissue. In the development of the *Acrobolbus* type, we have a combination of the conditions seen in the *Tylimanthus* and *Isotachis* types. The archegonial group is either developed on the upper half of the stem to begin with, or is displaced to the upper side by the growth of the ventral tissue. In either case, after fertilisation has occurred, this ventral tissue grows downwards, forming a cup which becomes extended to produce a tube, into the thickened lower end of which the sporogonial foot is plunged. In *Arnellia*, the marsupium begins in much the same way as in *Nardia geoscypha*, but the ventral swelling formed at the end of the archegonial branch becomes a shallow cup, to the bottom of which the archegonial group is carried, the calyptra remaining free right to the base of the cup, while the perianth and involucre are left at the mouth; growth is soon arrested, and the marsupium remains in this incipient stage. In *Harpanthus*, a similar cup-like marsupium is formed, but the calyptra is adnate to the inner surface of the cup; in *Adelanthus*, both calyptra and perianth are carried down into the short marsupium. Finally, in the genera *Acrobolbus*, *Calypogeia*, *Lethocolea*, *Symphyomitra*, *Kantia*, *Saccogyna*, and *Balantiopsis*, we get well-developed tubular marsupia, sometimes reaching a length of several centimetres and completely investing the mature sporogonium. In some cases the meristem at the base of the developing marsupium is covered by inactive tissue which, as Goebel has pointed out, resembles a root-cap in structure and behaviour. The interior of the marsupium is frequently lined by outgrowths bearing papillæ which secrete a gummy liquid (Fig. 51, V.), and the wall of the marsupium may be strengthened by a network of thick-walled cells.

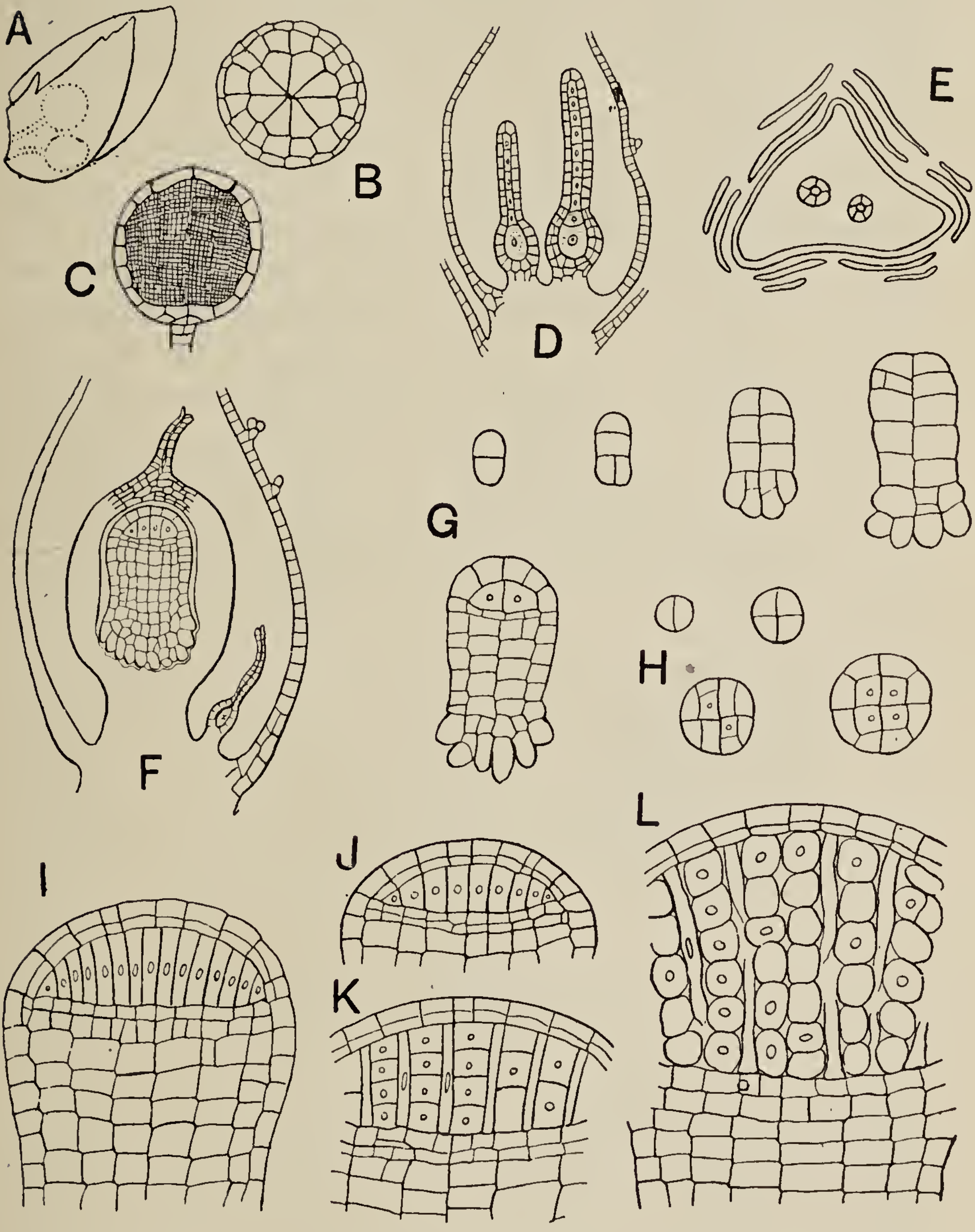


Fig. 52. *Frullania dilatata.* A, a perigonial leaf (male bract), from ventral surface, showing two antheridia; B, C, antheridium in apical view and in longitudinal section; D, longitudinal section of perianth with two archegonia; E, transverse section of same; F, longitudinal section of perianth showing embryo in fertilised archegonium, with unfertilised archegonium on the right; G, a series of longitudinal, and H, a series of transverse sections of embryos of different ages; I, J, K, L, longitudinal sections of older sporogonia, to show development of spores and elaters.

The Lejeuneaceæ, including *Frullania*, *Jubula*, and the Lejeuneæ, are sharply marked off from the remaining Acrogynæ in the structure and development of the sporogonium. The embryology of *Frullania* has been described and figured more completely than that of any other genus of Acrogynæ, having been investigated by Kienitz-Gerloff (49), Leitgeb (54), Leclerc du Sablon (52), and the writer (6). The first wall is transverse, the lower (hypobasal) cell then divides by a vertical wall and the upper (epibasal) cell by a transverse wall (Fig. 52, G). Each of the two upper cells then divides by two sets of vertical walls intersecting at right angles; meanwhile the two hypobasal cells also divide again by vertical walls, so that the embryo consists of three tiers, each with four cells. The hypobasal cells soon project and divide somewhat irregularly to form the blunt foot or haustorium which presses into the tissue forming the stalk of the archegonium. The cells of the uppermost tier divide by tangential walls into four inner cells (archesporium) with denser protoplasm than the four outer cells which form the capsule-wall. The middle tier divides by longitudinal walls separating eight outer cells from four inner ones; this tier produces the stalk and lower part of the capsule. The divisions in the four primary archesporial cells are extraordinarily regular and diagrammatic. At first only longitudinal divisions occur, until there is formed a lens-like mass of about two hundred cells, the central cells being longer than the outer ones (Fig. 52, I, J). These cells then become differentiated into two sets. Some divide transversely to form rows of spore-mother-cells; the others grow in length but remain undivided, forming long cylindrical cells attached to the inner surface of the capsule-wall above, and to the floor of the capsule below. The rows of cubical sporogenous cells alternate regularly with the long undivided cells, each of which will form an elater extending the entire depth of the capsule (Fig. 53, A). Each elater becomes flattened and trumpet-like at the lower end, and contains a single broad spiral band; there are about a hundred of them in a well-grown *Frullania* capsule, those nearest the centre being the longest. The structure of the two-layered capsule-wall is very characteristic: the cells of the outer layer have rod-like fibres on their lateral walls, especially at the angles between adjacent cells, while on the walls of the inner layer the thickenings form an irregular net work (Fig. 53, D). The seta is not so sharply marked off from the capsule as in most liverworts, for at the base of the capsule there is a mass of thin-walled tissue corresponding to the apophysis of a moss sporogonium, hence at dehiscence the four valves of the capsule do not become free right down to the point of junction with the cylindrical seta ; in systematic books the capsule of *Frullania* is therefore described as "opening for only two-thirds of its length." When the ripe capsule dries, the elaters contract and their lower ends become free from the floor of the capsule while their more firmly fixed upper ends remain attached to the inner surface of the capsule-wall. Then the wall splits from above downwards into four valves (Fig. 54) which spring outwards with explosive violence, the spores being flicked away to a distance of several inches by the sling-like action of the elaters which are suddenly bent outwards with the four valves.

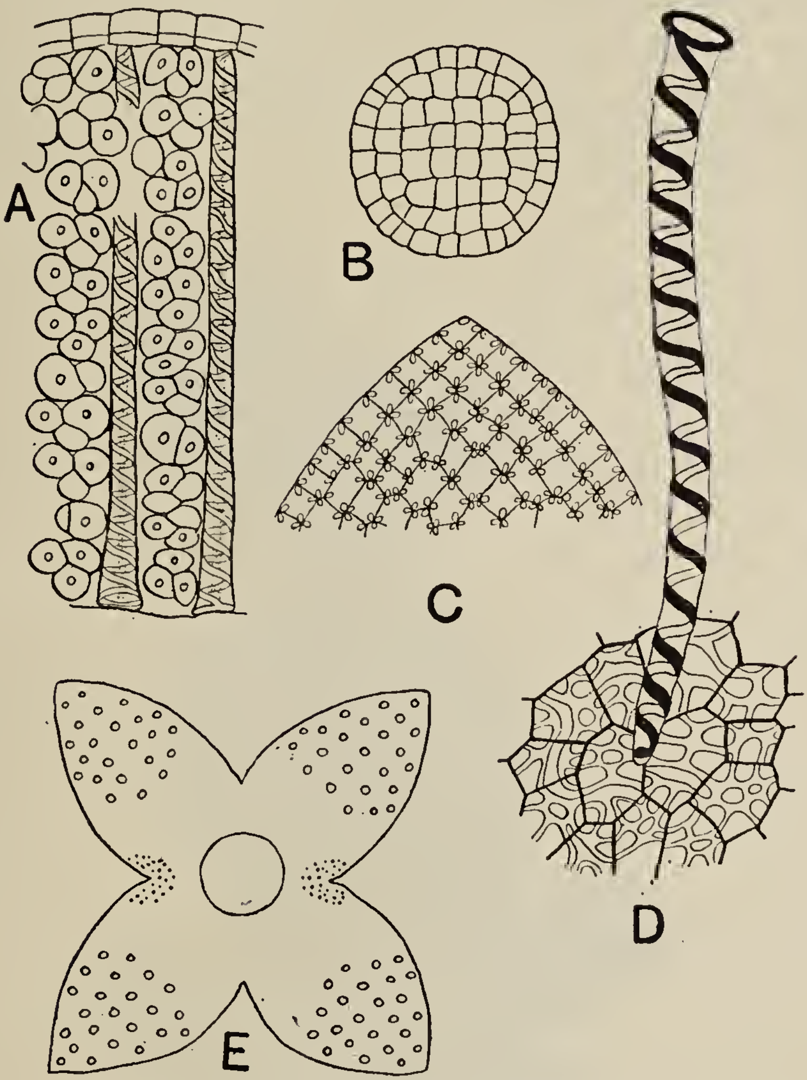


Fig. 53. *Frullania dilatata.* A, longitudinal section of well-grown capsule, with spore-mother-cells dividing ; B, cross section of seta ; C, part of wall of capsule (upper end of one of the four valves) seen from outer surface ; D, part of inner surface of capsule-wall, with an elater ; E, diagram (from Jack, 'Bot. Zeit.,' 1877) showing the arrangement of the elaters on the four valves of the capsule-wall, as seen from above.

In the remaining Acrogynæ, the elaters and spores never show the same relation to each other as in the Lejeuneaceæ, and frequently they are mingled quite irregularly. In many cases, however, they show a tendency to radiate from the base when the capsule is spherical, and to be arranged more or less horizontally around a central longitudinal axis when the capsule is oblong in form. In *Lepicolea*, most of the elaters are of the normal bi-spiral type and mingled with the spores, but from the base of the capsule there springs a tuft of much larger fixed elaters having a single spiral fibre; this exactly corresponds to the elaterophore of *Pellia* in both position and structure. Goebel (33) has recently shown that in *Gottschea splanchnophylla* there is a well-developed rod-like basal columella or elaterophore, corresponding in *structure* with the apical elaterophore of *Aneura* and *Metzgeria*, but resembling in *position* the basal tuft of fixed elaters in *Pellia*. With very few exceptions, the

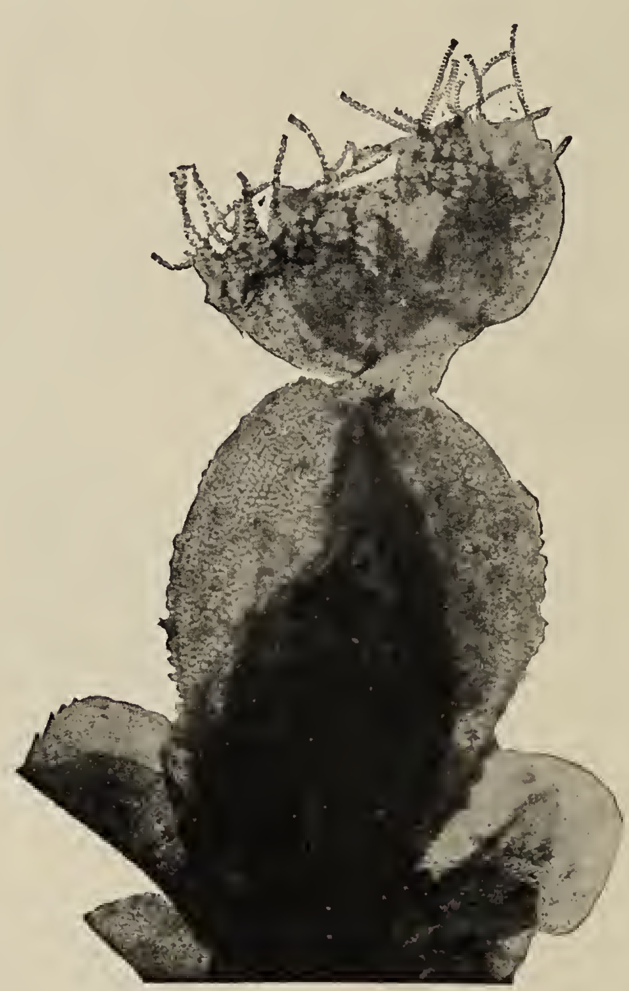


Fig. 54. *Frullania dilatata.* End of a female branch (dorsal view) with capsule, which has exploded and shed the spores, after having (by the elongation of the seta), broken out of the calyptra and the perianth. The calyptra, bearing the withered archegonium-neck, can be seen inside the perianth; the tubercles on the outer surface of the perianth are plainly shown on either side.

capsule-wall has well-developed fibrous thickenings in its cells, which are usually arranged in two layers. An apical cap or lens-like thickening of the capsule-wall, such as occurs in many Marchantiales and Anacrogynæ, is apparently never found in Acrogynæ, but the number of layers composing the capsule-wall is often more than two, and may be as many as eight.

The capsule-wall and the seta are remarkably constant in structure in the various genera and groups of genera, thus affording characters of considerable value in classification, and in some cases affording a useful clue to the probable inter-relationships of the orders. For instance the genera *Porella* and *Radula*, forming the two orders Radulaceæ and Porellaceæ, approach the Lejeuneaceæ even more closely in the structure of the capsule-wall than in the vegetative characters which led the older systematists (*e.g.*, in the Synopsis Hepaticarum) to unite these two genera into the tribe "Platyphylleæ" and place this next to the "Jubuleæ" (Lejeuneaceæ). Again, the genus *Pleurozia (Physiotium)* was placed with genera like *Lepidozia* and *Calypogeia* in the "Trichomanoideæ" of the Synopsis, while in Engler and Prantl it is given ordinal rank and brought close to the Lejeuneaceæ. *Pleurozia* differs from *Radula*, *Porella*, and the Lejeuneaceæ in that the capsule-wall consists of about eight instead of two layers of cells, but in other genera with a many-layered capsule-wall all the layers except the outermost one consist of flattened cells, while in *Pleurozia* the innermost layer has precisely the same type of thickening as the inner of the two layers in the Lejeuneaceæ. That is to say, the capsule-wall of *Pleurozia* has evidently been derived from the *Lejeunea* and *Frullania* type by the interpolation of several layers of narrow flat cells between the outer and the inner layer of more or less cubical cells, and the structure of the capsule supports the evidence drawn from other characters as to the probable relationship between *Pleurozia* and the Lejeuneaceæ.

In certain genera of Acrogynæ, the gametophyte shows a remarkable degree of dimorphism, in that the germinating spore produces a vegetative thalloid plant-body on which arise leafy shoots bearing the sexual organs. In two of these genera (*Metzgeriopsis* and *Pteropsiella*) the vegetative body is a flattened thallus resembling that of an *Aneura* or a *Metzgeria*, while in *Protocephalozia* it is a branching filamentous structure closely resembling the protonema of a typical Moss. In each case, the sexual organs are borne on leafy branches which have the typical Acrogynous characters, and the structure of these branches and of the sporogonium and its envelopes enable us to refer these aberrant genera to their systematic position in the group.

In *Metzgeriopsis* (*Thallolejeunea*) *pusilla*, an epiphyllous plant discovered by Goebel (28) in Java and investigated by him and also by Schiffner (70), the thalloid plant-body is ribbon-like, branched pinnately, and consists of a single layer of cells; each branch grows by a two-sided apical cell, as in *Metzgeria*. Along the margin of the thallus there arise appendages arranged in regular order and consisting of cell-rows; from their regular succession, these appendages may, perhaps, be regarded, as Goebel points out, as rudimentary leaves. The thallus is fixed to the substratum by rhizoids, and it is propagated asexually by gemmæ. The plant is diœcious, and may bear a considerable number of male or female leafy shoots, each of these shoots replacing an ordinary branch. Each sexual shoot grows by a three-sided apical cell, which is doubtless derived directly from the two-sided apical cell of an ordinary branch, and after producing one or two rudimentary leaves it proceeds to the development of large well-developed bilobed leaves which protect the sexual organs. The male catkin-like branches bear about ten perigonial leaves, each saccate at the base and having a pair of antheridia in its axil; the female branch has about six leaves, the largest two forming the involucre around the perianth. At the base of each sexual shoot, rhizoids are usually given off in a tuft.

In *Pteropsiella frondiformis*, discovered by Spruce in Brazil, growing on fallen leaves and decaying wood, the vegetative body is a strap-like thallus which resembles that of *Podomitrium* or the species belonging to the "Repentes" sections of *Blyttia* and *Symphyogyna*, rather than that of *Metzgeria*. It has a well-marked midrib about six cells thick, and on either side an expanded single-layered wing. Growth takes place by a three-sided apical cell, each lateral segment bearing papillæ which come to occupy the margin of the wing at regular intervals, while the ventral segments produce small simple amphigastria. From the midrib, on the lower side of the thallus, there arise sterile thalloid branches and also leafy sexual shoots. The male shoot has a stalk-like base continuous with the midrib of the thallus, and bears numerous male bracts in two lateral rows—the writer (5) has noted that in some cases the male shoot may resume vegetative "thalloid" growth after producing the antheridia, the apex growing out to form a flattened expansion on either side of the mid-rib or stem. The female branch bears a few involucral leaves in three rows, and finally the archegonial group surrounded by the perianth, these structures agreeing closely with the *Cephalozia* type.

Protocephalozia ephemeroides is closely allied to *Pteropsiella* and placed with it in the Cephaloziaceæ. Spruce, who discovered this curious little plant in Venezuela, growing on moist soil in shade and on mounds thrown up by mud-worms, says "I had already found a minute Phascoid moss (*Ephemerum æquinoctiale*) in similar sites; it is the only *Phascum* known to me that grows on the hot plains of the equator, and at first sight I took the *Protocephalozia* for a second species of the same genus, for I saw on the lumps of mould only a greenish confervoid film, with large perichætia standing out of it here and there—very like the *Ephemerum serratum* on our garden-pots in England. The prothallium of all Cephalozias is narrow and threadlike—very different from the suborbicular prothallium and propagula of *Radula*, *Lejeunea*, and many other Hepaticæ: and it approaches the nearest of any among Hepaticæ to the protonema of true mosses." The vegetative organs consist simply of branching cell-rows, exactly resembling the filamentous protonema of Mosses and differentiated into an underground portion in which the cells have smooth thin walls and no chlorophyll, and an aerial portion which tends to grow erect, is profusely branched, contains chloroplasts, and has the cell-walls covered externally with papillate thickenings. At certain points on this protonema, the branches remain short, develop an apical cell of the usual three-sided type, and give rise to the leafy sexual shoots. The plant has a tufted habit, the usually solitary female shoot arising from the base and the male shoots higher up on the branching filaments.

The classification of the Acrogynæ here suggested is based upon that proposed by Spruce in his classical work on the Hepaticæ of the Amazon and the Andes (78), with some slight alterations.

A. Leaves typically divided into a large upper and a small lower lobe, the latter usually rolled up or saccate; underleaves usually present; perianth usually with wing-like ridges, contracted at the apex to a tubular beak, and ruptured irregularly by the exsertion of the short-stalked capsule; elaters few, with a single spiral fibre, all fixed by their upper ends to the inside of the capsule-wall and extending to the floor of the capsule-cavity; archegonia from one to four (rarely more) in a group.

1.—LEJEUNEACEÆ. This is the largest family, including nearly 2,000 species of which the majority belong to the old genus *Lejeunea*, now broken up into about sixty genera. *Frullania*, the sub-genera of which should perhaps be treated as independent genera, is sharply distinguished from the Lejeuneas by its helmet-shaped water-sacs, though the genus *Jubula*, as shown by Evans (16), forms in various respects a connecting link between the Lejeuneas and the Frullanias. The most remarkable of the Lejeuneas is *Metzgeriopsis* (*Thallolejeunea*).

B. Leaves various as to form and insertion; perianth rarely with longitudinal wings; capsule usually long-stalked; elaters numerous and arranged in various ways but never fixed above or extending from roof to floor of capsule-cavity; each elater with two or more spiral fibres; archegonia always more than four, usually numerous, in a group.

a. Leaves typically with two lobes folded upon each other and differing in size and often also in form.

2.—PORELLACEÆ. Lower leaf-lobe small, flat or concave, but never saccate or bearing rhizoids; underleaves present; perianth dorsiventrally compressed; capsule-valves not extending to base of capsule. Only genus *Porella*.

3.—PLEUROZIACEÆ. Upper leaf-lobe larger than lower, the latter saccate and often provided with a trap-door mechanism; underleaves absent; perianth elongated and folded. Only genus *Pleurozia*.

4.—RADULACEÆ. Upper leaf-lobe much larger than lower; rhizoids borne in tufts on the lower leaf-lobes instead of on the stem; underleaves absent; perianth dorsiventrally compressed, smooth. Only genus *Radula*.

5.—SCAPANIACEÆ. Upper lobe of leaf smaller than lower; underleaves small or absent; perianth either cylindrical or dorsiventrally compressed, usually folded. Chief genera *Scapania*, *Diplophyllum*, *Gottschea*, *Balantiopsis*.

b. Leaves either entire, or with toothed or lobed margins, or deeply lobed, but with the lobes equal in size and form.

6.—PTILIDIACEÆ. Leaves generally with several long teeth or lobes; underleaves always present and resembling the leaves in form and size; perianth with longitudinal folds and often concrescent with involucre. About a dozen genera, including *Ptilidium*, *Isotachis*, *Herberta*, *Polyotus*, *Trichocolea*, *Blepharostoma*.

7.—Cephaloziaceæ (*Trigonantheæ*, Spruce). Leaves usually incubous; leaf-margin rarely entire, usually lobed or toothed; underleaves usually present, but smaller than the leaves and of different form; perianth usually hypogonanthous (*i.e.*, triangular in cross-section, with two dorsal angles and a ventral angle). About thirty genera, including *Cephalozia*, *Protocephalozia*, *Pteropsiella*, *Zoopsis*, *Lepidozia*, *Anomoclada*, *Mytilopsis*, *Micropterygium*, *Arachniopsis*, *Bazzania*, *Adelanthus*, *Marsupidium*, *Kantia*, etc.

8. Lophoziaceæ (*Epigonantheæ*, Spruce. Leaves succubous or transversely inserted, entire or two-lobed; underleaves absent or small; perianth usually epigonanthous (*i.e.*, triangular in cross-section, with a dorsal angle and two ventral angles). About thirty genera, including *Lophozia*, *Haplozia*, *Nardia*, *Gymnomitrium*, *Marsupella*, *Plagiochila*, *Notoscyphus*, *Southbya*, *Arnellia*, *Tylimanthus*, *Lethocolea*, *Symphyomitra*, *Calypogeia*, *Saccogyna*, *Acrobolbus*, etc.

In the foregoing scheme, which is admittedly to a large extent artificial and provisional, I have suggested the elevation of the eight groups, which Schiffner (68) treats as sub-orders of Jungermanniaceæ, into independent orders. The only sharply marked and really natural families are the Lejeuneaceæ, Porellaceæ, Pleuroziaceæ, and Radulaceæ; the remaining four families are closely connected with each other and therefore difficult to characterise. This is especially the case with the Lophoziaceæ and the Cephaloziaceæ, which should, perhaps, be merged into one family. In these two families the perianth is quite as often as not a smooth or folded cylinder, neither distinctly "epigonanthous" nor "hypogonanthous"; the leaves are often quite as distinctly bilobed in Lophoziaceæ as in Cephaloziaceæ; the acrocarpous or pleurocarpous position of the archegonial group (and therefore of the sporogonium) varies in closely allied genera and even in species of the same genus (e.g., *Cephalozia*). That is, the two families cannot be kept apart by any of the characters generally used to distinguish them. The difficulty of framing a natural classification is increased by the occurrence of many features which can only be regarded as examples of homoplasy. Among these parallel developments, may be mentioned the following, which are found in widely separated genera and families:—open water-pitchers (*Radula*, *Polyotus*, *Frullania*, etc.); closed pitchers with a trap-door or valve mechanism (*Pleurozia*, *Colurolejeunea*); paraphylls (*Gottschea*, *Trichocolea*, *Stephaniella*, *Marsupidium*); cœlocauly—the penetration of the stem by the sporogonium (*Gottschea*, *Trichocolea*, *Polyotus*, etc.); the formation of marsupia of various structural types (*Tylimanthus*, *Balantiopsis*, *Acrobolbus*, *Kantia*, etc.).

THE INTER-RELATIONSHIPS OF THE ACROGYNÆ.

In discussing the inter-relationships of the Anacrogynous Jungermanniales, reasons were brought forward to support the view that the division of the Jungermanniales into Anacrogynæ and Acrogynæ is a purely artificial one. It was also suggested that the Anacrogynæ have arisen from a thalloid ancestor, and that the differentiation of stem and leaves has taken place in several diverging lines of affinity, starting from an undifferentiated thallus. On these views we must assume that the Acrogynæ have arisen from the Anacrogynæ, and of the two main series of Anacrogynæ it would appear that the *Pellia* series offers the natural starting-point for the Acrogynæ, since it is in the higher members of the *Pellia* line—in genera like *Fossombronia*—that we find the sharpest differentiation into stem and leaf.

The Lejeuneaceæ are so sharply distinguished from all the other Acrogynæ in the structure of the capsule, that some writers have inclined to the view that this group has arisen independently and that the Acrogynæ form a polyphyletic group, derived from the Anacrogynæ along two independent lines. Spruce was so deeply impressed by the marked characters of the Lejeuneaceæ that he divided the Jungermanniales into two groups—the "Jubuleæ" or Lejeuneaceæ forming one group, while his group "Jungermannieæ" included all the remaining forms, both Acrogynous and Anacrogynous. Schiffner (68) considered that the sporogonium of the Lejeuneaceæ shows such a degree of resemblance to that of the Aneuraceæ that he suggested the independent origin of the Lejeuneaceæ from a *Metzgeria*-like form, all the remaining Acrogynæ being derivable from a form like *Fossombronia*. This view is adopted by Lotsy (60), who reproduces the general phylogenetic scheme suggested by Schiffner for the Acrogynæ. It is only fair to add that neither of these writers discusses the question in detail, and that both put their views forward in a tentative fashion. A careful comparison of the structure and development of the gametophyte and sporogonium in the Lejeuneaceæ and the Aneuraceæ shows that there are two points of apparent resemblance between these groups.

Taking first the sporogonial characters, which led Schiffner to suggest the possible origin of Lejeuneaceæ from Aneuraceæ, we find the resemblances are purely superficial. It is true that in both series elaters remain attached by their upper ends to the four valves of the dehisced capsule-wall, and that there is consequently a general similarity in the mechanism by which the spores are scattered. There are, however, fundamental differences in the structure and development of the capsule in the two families. In the Aneuraceæ, we find a solid mass of sterile tissue, forming an incomplete apical columella or elaterophore and splitting at dehiscence into four portions which remain fixed to the capsule-valves; some of the elaters are attached to this elaterophore, the rest being free and mingled with the spores. In Lejeuneaceæ, on the other hand, there is a regular alternation between (1) elaters fixed apically and extending the entire depth of the capsule-cavity, and (2) longitudinal rows of spores; there is no elaterophore, and all the elaters are fixed. The occurence of elaters fixed by their upper ends to the inside of the capsule-wall in various genera of Acrogynæ widely removed from the Lejeuneaceæ in the current system of classification forms an additional argument, if any be necessary, against the existence of any close connexion between the Aneuraceæ and the Lejeuneaceæ as regards the structure of the sporogonium. The Lejeuneaceous capsule is, in fact, much more readily derived from that of, say, *Cephalozia* or *Lepidozia*, than from that of *Aneura* or *Metzgeria*. In *Cephalozia*, *Lepidozia*, and several other genera, most, if not all, of the elaters are fixed by one end to the capsule-wall and radiate towards the centre and the base of the capsule-cavity (Fig. 50, IV.), and from this type the arrangement characteristic of the Lejeuneaceæ can easily be derived. The resemblances between the Aneuraceous and Lejeuneaceous types of capsule-structure appear, in short, to be entirely illusory.

Much more striking is the resemblance between the Aneuraceæ and Lejeuneaceæ in the early stages of development of the gametophyte. Except for the absence of a midrib, the thalloid vegetative plant-body of *Metzgeriopsis*, which may be regarded as a persistent protonema, agrees exactly with the thallus of a *Metzgeria*. The early stages in germination of the spore are precisely alike in *Metzgeria* and the Lejeuneas; in both cases, after one or two transverse divisions have taken place in the short germ-tube, the distal cell gives rise to a two-sided apical cell and a ribbon-like protonema is formed. In *Metzgeria* and in *Metzgeriopsis* the protonema continues to grow as a flat thallus; in *Metzgeria* a midrib is formed and the protonema develops directly into the adult thallus, while in *Metzgeriopsis* the persistent protonema or thallus gives rise eventually to the leafy sexual shoots. Moreover, *Metzgeria* and the Lejeuneæ agree in producing discoid gemmæ, but in this respect the two genera simply illustrate what appears to be a general rule in the Hepaticæ, namely, that the protonema and the gemmæ of any given species usually show a close resemblance in form.

As an indication that too much stress should not be laid upon the mode of germination and the form of the protonema in the different groups of Hepaticæ, it may be pointed out that there are great variations in this respect amongst allied forms. The germination of a considerable number of Hepaticæ has been described by Grönland (37), Leitgeb (56), Campbell (3), Frau Lampa (51). Douin (9), Goebel (32), and others. In Hepaticæ, as in Mosses, the development of the gametophyte is "heteroblastic," since there is first formed a protonema or "pro-embryo" of simple form, and from this the adult plant arises, usually from a terminal cell which becomes the apical cell of the plant-body. As a rule, the spore contents grow out to form a positively heliotropic and usually unbranched filament or germ-tube in the first instance, and the apical cell of the adult plant may either arise from the terminal cell of this filament (most Acrogynæ), or the formation of a germ-tube may be more or less completely suppressed so that the protonema forms a cell-surface or disc; the young plant arising from one of the marginal cells. A germ-disc is formed directly from the spore in *Radula*, for instance; in *Frullania* and *Porella*, divisions occur in all directions of space, producing a solid ovoid protonema instead of a discoid cell-surface. In various other genera of Acrogynæ, we find transitions from the germ-tube to the germ-disc types of protonema; sometimes both types are found in the same species.

In the other groups of Hepaticæ, we find similar diversity in the form of protonema. Among the Anacrogynæ, *Aneura* resembles *Metzgeria*, except that sometimes the protonema is at first filamentous and may even undergo branching before giving rise to a cell-surface and developing into the adult thallus. In *Pellia*, an ovoid cell-mass is formed by the germination of the spore while still within the capsule, a hyaline cell at one end producing the first rhizoid when the spore is shed, while the growing-point arises from the other end; or both ends may produce a rhizoid, while the growing point arises in the middle of the protonema. In *Blasia*, the cell-mass from which the thallus arises may either be produced from the terminal cell of a germ-tube, or the latter may be suppressed so that the cell-mass arises directly from the spore. The germination of *Fossombronia*, according to Frau Lampa, is somewhat remarkable—the end-cell of the germ-tube gives rise to a three-sided apical cell, producing three rows of leaves, though the apical cell of the adult plant is two-sided and the leaves are in two rows.

In the Marchantiales, *Fegatella* resembles *Pellia* in that the spore germinates before leaving the capsule, forming an ovoid cell-mass, and Frau Lampa states that when the multicellular spore, or protonema, is set free it grows at first by a three-sided apical cell and is cylindrical, but later acquires dorsiventrality and gives rise to the adult thallus. The same writer also describes the cell-mass formed in various genera of Marchantiales by division of the end-cell of the germ-tube, as growing at first by a three-sided apical cell and producing three rows of leaves, which are especially definite in *Preissia*.

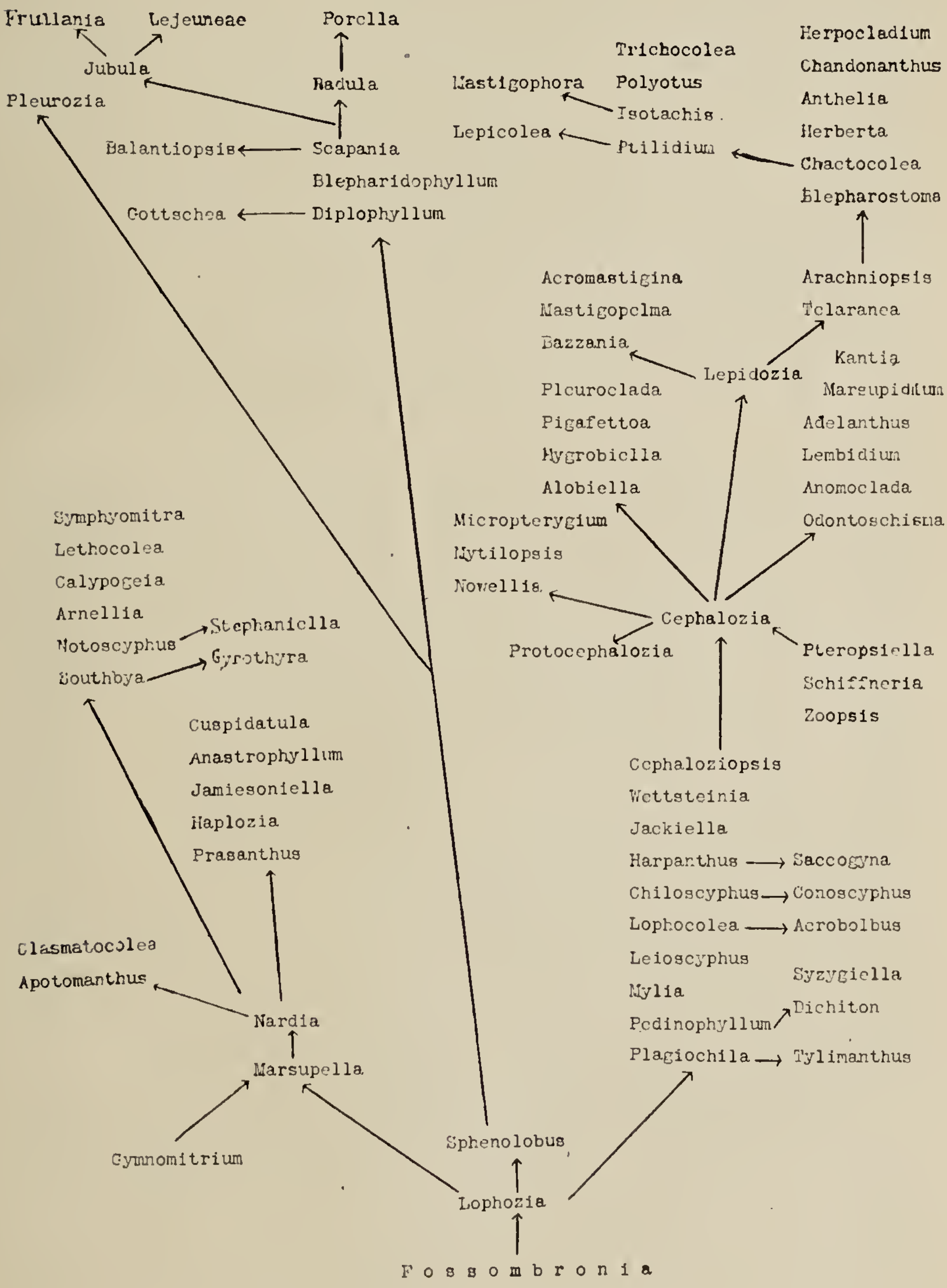
As already stated, there are many cases in which the form of the Hepatic protonema varies between the two main types—the filamentous and the discoid—in the same species. Moreover, it has been shown, by Schostakowitsch (74) and others that the structure and duration of the protonema can be altered at will by controlling the external conditions under which the spore germinates, and that light-intensity is the most important of these conditions. For instance, the normally short-lived filamentous protonema of *Cephalozia*, *Chiloscyphus*, etc., can be cultivated for many months in feeble light without producing leafy shoots; the protonema branches freely, like the protonema of a Moss or the filamentous vegetative body of *Protocephalozia*. In the Marchantiales feeble light inhibits the formation of the germ-disc and therefore of the adult thallus; if a germ-disc has been formed, reduction in light-intensity causes it to give out filaments, on which further germ-discs are produced on exposure to stronger light, and so on. Again, if the protonema of a leafy Hepatic has already given rise to the young leafy shoot, exposure to weak light inhibits the development of the adult type of leaf, so that we get a slender plant with rudimentary leaves; this state of things occurs normally in *Zoopsis*, a genus allied to *Cephalozia*. Without going further into details, it may be said that all the phenomena of arrested development which can be induced artificially, or which occur occasionally, in almost any Liverwort, also occur regularly in nature in certain species.

However, we shall discuss later certain questions bearing upon the phylogeny of the Bryophyta in general which arise from the phenomena of juvenile stages and of naturally occurring as well as artificially induced variations in the form of the gametopyte. There is much need for further observations on the germination of Hepaticæ, and for work in experimental morphology in this group. From what has been set forth here, it would appear that the resemblances between the Aneuraceæ and Lejeuneaceæ in the form of the protonema cannot be regarded as indicating any real link between the two groups. We are therefore driven to the conclusion that the Acrogynæ form a monophyletic series.

A careful survey of the Acrogynæ suggests that the following may be regarded as relatively primitive gametophytic characters:— leaves symmetrically bilobed more or less deeply, and either flat or only slightly folded; underleaves present; archegonia borne on the main axis; perianth free from the involucre and either cylindrical or corresponding to three flat leaves carried up by common basal growth; protonema filamentous. On the other hand, we may regard as advanced or specialised characters the complete absence of lobing from the leaf, or on the contrary its division into several deep lobes, or its division into two lobes of very unequal size; the absence of underleaves; the restriction of the archegonia to special short branches; the fusion of the perianth with the involucre, lateral or dorsiventral flattening of the perianth, and the development of wings on its exterior; discoid protonema; and, finally, various elaborations such as the formation of pitchers, paraphylls, marsupia, etc. Many of these advanced and specialised characters have arisen independently in different lines of affinity, and are to be classed as parallel developments.

Assuming that the Acrogynæ have arisen from a *Fossombronia*-like type, it is probably among the Lophoziaceæ or the

Cephaloziaceæ that we should look for a form presenting the greatest resemblance to *Fossombronia*, and, at the same time, the most primitive Acrogynous characters. On the whole, perhaps the genus *Lophozia* may be selected as a good starting-point for the evolution of the Acrogynæ. In *Lophozia*, the branching is practically dichotomous, the leaf-insertion varies from transverse through succubous to nearly longitudinal, the leaves are more or less deeply and symmetrically bilobed, the underleaves are small



Phylogenetic scheme of the *Acrogynæ*.

(in some species absent), the archegonia are developed on the main shoots, the perianth is cylindrical and free from the involucre. From *Lophozia* we can trace three main lines. (1) One line leads directly through *Sphenolobus* to the Scapaniaceous genera *Diplophyllum* and *Scapania*, in which the leaves are deeply lobed, the upper lobe being smaller than the lower and the insertion succubous. (2) A second line leads through a long series of genera with relatively simple characters (*Plagiochila*, *Lophocolea*, etc.) to genera to in which the archegonia are shifted on to short lateral branches (*Chiloscyphus*, *Harpanthus*, etc.), and which in this and other respects form a transition to the Cephaloziaceæ through intermediate types like *Cephaloziopsis*, *Cephaloziella*,, and *Cephalozia* itself. Several marsupial genera arise from this line, e.g., *Tylimanthus* and *Acrobolbus*, which are allied to *Plagiochila*, and *Saccogyna* which resembles *Harpanthus* in vegetative characters. (3) The third line is marked by the reduction in size of the perianth, fusion of perianth with involucre, and the development of marsupia; this line begins with *Marsupella*, and leads through *Nardia* to the marsupial genera *Southbya*, *Calypogeia*, *Lethocolea*, etc.

In the *Cephalozia* series, three lines start from *Cephalozia* itself. (1) One of these is marked by more or less far-reaching reduction of the leaves, leading to forms like *Zoopsis* and *Pteropsiella*, the latter becoming thalloid owing to the "fusion" of the leaves with the stem, while *Protocephalozia* has a persistent filamentous protonema, leaves being produced only on the sexual shoots. (2) A second line, in which the leaves are only slightly lobed or quite entire and the archegonia are restricted to very short ventral branches, leads through *Odontoschisma* and *Adelanthus* to the marsupial genera *Marsupidium* and *Kantia*—the only marsupial forms in the Cephaloziaceæ. (3) The third line, characterised by the division of the leaf into increasingly numerous and deep lobes, leads through *Bazzania* and *Lepidozia* to *Arachniopsis* and *Telaranea*, which closely resemble the Ptilidiaceous genus *Blepharostoma* and form a transition to this family.

The Ptilidiaceæ, though a small family, shows several diverging lines of development, all of which appear to end blindly. In the majority of the genera, the archegonial group is terminal on the main axis; in the others (*Ptilidium*, *Lepicolea*, *Mastigophora*, *Isotachis*) it is on a short branch, but this is lateral—not ventral, as in the Cephaloziaceæ. A very marked character of the family is the agreement in form and size between the leaves and the under-leaves—a character found only in *Lepidozia* among the Cephaloziaceæ. With the latter family the Ptilidiaceæ agree in the form of the perianth, which is either cylindrical or triangular with one angle ventral; this sharply separates the Ptilidiaceæ from the Lophoziaceæ, in which the perianth when triangular has one angle dorsal. In this small but interesting and diversified family we find a number of features which recur in various other families of Acrogynæ, and which are examples of parallelism, *e.g.*, the development of paraphylls in *Chandonanthus* and *Trichocolea*, the *Frullania*-like pitchers of *Polyotus*, the "midrib" of elongated cells in the leaves of *Herberta*.

The Scapaniaceæ, which may be derived from a *Lophozia*-like type, present various features which recur in other families, *e.g.*, the winged leaf *Gottschea* (cf. *Micropterygium*) and the marsupium of *Balantiopsis*. The most marked vegetative peculiarity of this family is the small size of the dorsal as compared with the ventral lobe of the leaf. However, in some species of *Scapania* the two lobes are equal in size, or nearly so.

The remaining four families agree with each other and differ from the rest of the Acrogynæ in the deep division of the leaf into a large dorsal and a small ventral lobe, the two lobes being sharply folded against each other, and in the discoid form of the protonema and of the gemmæ. In none of these four families is a marsupium formed, and the perianth is never concrescent with the involucre. Each family presents strongly marked characters of its own, but they are probably connected with the other Acrogynæ through *Radula* and *Scapania*. In some species of both these genera, the two lobes of the leaf are equal in size, and the two genera further agree in having a dorsiventrally flattened perianth. *Porella* agrees with *Radula* in general habit, but it has under-leaves, the archegonia are on special short branches, and the upper end of the seta is expanded to form an apophysis. *Jubula* is probably related to *Porella*, and from *Jubula* we can derive on one hand the genus *Frullania* and on the other the Lejeuneæ. *Pleurozia* is a somewhat isolated genus, and it is probably more nearly related to the *Lophozia* series than to *Porella* and *Radula*, with which it is associated in the scheme of classification.

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AN INVESTIGATION OF A SPECIES OF *SAPROLEGNIA*

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[Plates I. and II.]

Introduction.

In January, 1910, a plentiful supply of *Saprolegnia* came to hand, from dead fish in the pond in the Botanical Garden of the University of Bristol, and specimens brought into the laboratory showed a plentiful crop of zoosporocysts, several of which were observed discharging zoospores. I thought this a good opportunity for working through the life history of a species of *Saprolegnia*, and the process of isolation into pure culture was therefore at once commenced.

Method of culture and isolation.—The isolation in the first place was carried out by means of plate cultures on an extract of beef with gelatine after the manner described by Kauffman ('08.) The method of preparation, however, was slightly different as by repeating his process the hæmoglobin was found to coagulate in the gelatine. The method then used was as follows:—

Half-a-pound of beef without any fat was cut up in small pieces and extracted with water at 27°C for four hours; the whole of the extract was then allowed to simmer in a beaker in a water bath for half-an-hour, the liquid pressed off and the meat strained through muslin. The extract was now boiled for ten minutes to completely coagulate all the hæmoglobin in the solution, and then filtered through filter paper; a clear solution was then obtained and this was made up to 1,000 c.c with more water and 100 gm. gelatine added. The whole was heated in a water bath till all the gelatine was dissolved and then drawn off into test tubes which were sterilized by the ordinary method of intermittent heating.

The Petri dishes used were sterilized by dry heat 120°—140°C for twenty minutes.

The contents of some of the test tubes was then remelted in a water bath and transferred with the usual precautions to the sterile Petri dishes. In this way sterilized plates of beef extract gelatine were prepared, which were used throughout for all isolation processes.

A small piece of mycelium from one of the dead fish was then teased off with needles and washed in sterile distilled water to free it from some of the bacteria and infusoria which were so abundant on the specimens taken from the pond. The mycelium was then transferred to the centre of one of the sterile dishes and left till next day when a considerable growth was found to have taken place, forming a circular patch 1½ inches in diameter. The extreme end of this mycelium was then removed, at first by cutting with a scissors sterilized in absolute alcohol, but later it was found better to use a stout piece of platinum wire in a glass rod, the wire being bent at right angles for about one-eighth of an inch at the end. This small implement was found to be very efficient. It could easily be sterilized by passing through a flame, and it did not leave clean cut ends on the hyphæ as in the case of the scissors, but severed them by pressure.

In spite of all precautions the bacterial growth was very rapid, owing perhaps to the rather warm temperature of the room, which was probably near the optimum for the bacteria. If the cultures could have been kept at a lower temperature the rate of growth of the bacteria would have been much slower in proportion to that of the fungus. After two weeks of culture by this method, cultures were obtained free from all bacteria. The mycelium itself produces a decomposition of the gelatine due to the presence of proteoclastic enzymes in the hyphæ, and after five days' growth complete liquefaction results. The mycelium formed on the plates was entirely vegetative, consisting of slender branched unicellular cœnocytic hyphæ. When once obtained pure it was found sufficient, for the retention of the stock, to start a new culture every other day.

In order to study the methods of reproduction cultures were made on small pieces of white of egg, hard boiled pieces of fish or the skin of fish, pieces of beef, and on dead flies, all sterilized in test tubes in the usual way. With egg, fish and beef, the method of culture was as follows:—A small piece of the medium was placed in a sterilized Petri dish, then a tube of sterile distilled water added. Then a small piece of mycelium from a culture of beef-extract gelatine two days' old was removed with the platinum hook and placed on or near the medium in the Petri dish. After an interval of one day a fringe of hyphæ was found all round the medium. With flies the cultures were made in small sterilized glass beakers, half filled with distilled water, upon which the flies were floated, after washing in absolute alcohol and distilled water.

After one day's growth, or sometimes later, a small piece of the medium with attached hyphæ was teased off with two platinum needles, and transferred to a hanging drop culture in a Ward's tube or glass ring slide. A method of blotting paper wads, which could be kept moist by a blotting paper syphon was found to act very well, and cultures could thus be kept going for a week with care. The hanging drop cultures could then be kept under the microscope for observation. Nearly all the drawings were made from living material in hanging drop culture.

On examining the various cultures made in this way, very great variation was found in the methods of formation, discharge, and in the subsequent fate of the zoospores. At first it was thought the cultures could not be pure, but this was hardly likely, as these phenomena were observed in cultures which for three weeks had been daily isolated with the sterilized platinum hook from the extreme edge of the mycelium of the previous day's growth. In many cases two or more of the variations to be described were found in the same hanging drop.

Up to the present time, in spite of growing the culture under a great variety of conditions, no signs of sexual organs have been found, although a great variety of asexual forms of reproduction have been noted.

ANALYSIS OF GENERA.

The work was started originally with the idea of repeating Kauffman's work on the variability of sexual organs grown under various conditions of culture. These, however, I have entirely failed to obtain, the variability has been entirely with the asexual forms of reproduction. In order that these should be more easily followed a short analysis of genera is given, which is based upon variations in the asexual method of reproduction, and is compiled from the papers of Hartog ('95), De Bary ('88) and Cornu ('72).

Saprolegnia.—Sporocysts born terminally on the hyphæ; after discharge a new sporocyst grows up inside the wall of the old one. Zoospores are discharged in a motile state and swarm actively for a short time, then come to rest and become spherical, encyst, then later become motile again, leaving their cyst walls empty and swarming actively. This period of swarming lasts much longer than the first; on coming to rest zoospores germinate directly into hyphæ. Oospores one to many; oocyst never completely filled.

Leptolegnia.—Asexual methods the same as in *Saprolegnia*, but there is only one oospore, which completely fills the oocyst.

Leptomitus.—This genus resembles *Saprolegnia* closely, but the sporocysts are frequently multiple. This is regarded by many as a mere form of *Saprolegnia* as *S. torulosa* shows septae, and is regarded by De Bary as only a modification of *S. ferax*. Cornu describes this as occurring in forms of *Achlya*.

Pythiopsis.—Zoospores on discharge resemble those of the second motile stage of *Saprolegnia*; on coming to rest they germinate directly, without any second swarming. Zoosporocysts arise from branches of the main hyphæ, in cymose order, or in a chain one behind the other. The new sporocysts never grow up inside the discharged sporocyst wall. On other points the genus resembles *Saprolegnia.*

Achlya.—Zoospores motile on discharge from the sporocyst, but they immediately collect at the mouth, encyst and form a group of spores. After resting some time, the spores leave their walls and become actively motile. The new sporocysts arise from the base of the old ones, forming a sympodium.

Aphanomyces.—This genus resembles *Achlya* generally, but the zoospores have no cilia and are formed in a single row in a very narrow sporocyst. Discharge is brought about by the amœboid crawling of the zoospores from the sporocyst. Encystment takes place at the mouth of the sporocyst. There is a second motile stage with normal zoospores after a period of rest. The new sporocyst grows up within the wall of the old one.

Dictyuchus.—The zoospores encyst within the sporocyst. The motile spores later emerge through both the sporocyst wall and their own cyst wall.

Thraustotheca.—The zoospores encyst within the sporocyst wall, which then breaks down, leaving a mass of encysted spores, from which the motile swarmers are formed.

Aplanes.—This genus resembles *Dictyuchus*, but the spores germinate *in situ*, within the sporocyst, without any motile stage.

A "*Dictyuchus*-form" is shown, by some species of *Saprolegnia* and *Achlya* in cases where the sporocysts fail to discharge their zoospores. In this case encystment takes place within the sporocyst. The spores may later be discharged in the second motile stage, or they may germinate *in situ* without any such motile stage. In either case such a sporocyst is known as a "Dictyosporocyst."

SPECIAL CHARACTERISTICS OF SAPROLEGNIA.

Certain phenomena may now be specially referred to, which are characteristic of large sections of the Saprolegniaceæ and which have been employed in the effort to establish a system of genera upon the asexual reproductive characters.

Diplanetism.—This term is applied to describe the occurrence of two motile stages in certain species and genera. The two forms of zoospore are different. The first form of zoospore is ovoid with two terminal equal flagella. The second form is slightly kidney shaped, with two unequal lateral flagella. Both forms have one or more contractile vacuoles. The second form of zoospore resembles that which is characteristic of the Peronosporeæ.

Adelphotaxy.— A term used to describe the mutual attraction for each other, sometimes shown by the zoospores when at close quarters. This is exhibited in the case of *Achlya* and yet more strongly in the genera in which no discharge of the zoospores takes place. It is also held accountable for collection of the swarm spores into clusters.

The formation of gonidia.—Gonidia, resting sporocysts or gemmæ occur in some species of *Saprolegnia*, *Achlya* and *Aphanomyces.* They resemble the first stage in the development of the sporocyst after the formation of the septum and they are able to remain for a long period without change. On germination they may either develop vegetative hyphæ or they may develop into normal sporocysts. In many cases they become completely separated from the hyphæ on which they were formed.

The formation of chlamydospores.—Chlamydospores closely resemble gemmæ or resting sporocysts, but they produce on germination a hypha, which terminates in a sporocyst, or, in some cases, a secondary gemma.

SUMMARY OF A CLASSIFICATION OF THE SAPROLEGNIACEÆ.

(Based on the asexual forms of reproduction.)

Zoospores encyst after swarming from sporocyst - - A.
" " at mouth of sporocyst - - - - B.
" " within the sporocyst - - - - C.

A.	(*a*). New sporocyst grows up inside the old one; diplanctic	Several Oospores.	1. *Saprolegnia.*
		One Oospore.	2. *Leptolegnia.*
	(*b*). Sporocysts, elongated and multiple; diplanetic - - - - - -		3. *Leptomitus.*
	(*c*). New sporocysts arise in cymose order; only the second motile form present - - -		4. *Pythiopsis.*
B.	(*a*). Sporocysts arise in cymose order - - -		5. *Achlya.*
	(*b*.) New sporocyst grows up inside the old one. Zoospores amœboid on first discharge - - - - - -		6. *Aphanomyces*
C.	(*a*). Wall of sporocyst breaks down after encystment, liberating a mass of encysted spores - - - - - -		7. *Thraustotheca*
	(*b*). Wall of sporocyst remains after encystment. Zoospores break through the wall - - - - - -		8. *Dictyuchus.*
	(*c*). Wall of sporocyst remains and spores germinate directly within it. No discharge, no motile stage - - - - - - - -		9. *Aplanes.*

FORMATION OF THE NORMAL SPOROCYST.

Before proceeding to describe the various divergences from normal sporocyst structure, seen in the species under observation, an account is given of the normal method of formation and discharge of a sporocyst based chiefly upon the work of Hartog and Humphrey, as their account substantially agrees with my own observation.

An ordinary vegetative hypha consists of a single cell-wall with a parietal lining of granular protoplasm containing numerous microsomes, and some cellulin corpuscles, enclosing a central vacuole filled with sap.

The first sign of formation of a sporocyst is the arrest of the apical growth of the hypha. The protoplasm continues to flow slowly towards the apex, causing the end to become densely filled with granular protoplasm and also a slight swelling of the walls. At first a gradual transition is seen from the dense granular protoplasm in the swollen end to the less dense protoplasm of the basal hypha; later on a clear line of division is seen, consisting of a band of hyaloplasm or clear protoplasm without any granules. This ring of hyaloplasm, by a process of condensation from its inner circumference, forms a transverse septum or disc sharply separated from the basal hypha.

The sporocysts may be of three kinds :—

(1). Full sporocysts, usually very small and with no central vacuole.

(2). Normal sporocysts, with a thick parietal layer of protoplasm enclosing a central vacuole.

(3). Starved sporocysts with a thin parietal layer enclosing a very large vacuole.

The granular protoplasm of the sporocyst is at first uniform, but later shows a number of splits reaching from the central vacuole nearly to the wall; the number of splits increases till a honeycomb network is formed with protoplasmic bridges traversing the strands of the network. Later these connecting strands disappear, leaving a number of spore-origins, each with one nucleus, as the meshes in a network. The spore-origins now contract, thus widening the space between them and severing any remaining protoplasmic strands. The surface of the origins now becomes smooth instead of granular.

The origins now expand again and come into close contact with one another; some (Büsgen, Rothert) assert that fusion occurs, but in some cases a clear septum has been seen, reaching to the wall of the sporocyst. The origins now become spores. At this stage Rothert and Hartog describe the exudation from the sporocyst of a substance which is attractive to bacteria, accompanied by a slight contraction of the sporocyst. As the spores become separated off vacuoles appear in each. In outline they are warty and often small pieces of protoplasm become separated off from them to fuse again later. A similar state of things is recorded by Rothert and De Bary as occurring during formation of the oospheres within the oocyst.

Each zoospore now slowly develops two cilia. The front spore usually has its cilia directed towards the opening. As the cilia grow out, they show a rhythmic undulating motion, and the whole spore is seen rocking within the sporocyst.

The mature zoospores show one to three vacuoles, one or more of which show rhythmic contraction. A slight process grows out from the sporocyst, through which discharge will take place, the cellulose cap of the process becomes faint in outline as the front spore approaches it, and finally disappears. Discharge then occurs through the opening. In some cases the spores seem to press against the wall to cause it to open outwards. In *Saprolegnia* the early spores swarm out very actively, but the later ones as they move out are very inactive, and sometimes the last one or two do not leave the sporocyst.

Asexual Reproduction in Species Under Observation.

In the species with which the present investigations have been carried out the most common type of sporocyst was that of a *Saprolegnia* with diplanetic zoospores; this has been taken as the typical form for the species. Besides this typical form eight variants on the normal type have been found to occur in the various cultures under different conditions.

The cases observed were as follows:—

(1). *Typical Case.* A small piece of fish (or other medium) bearing vegetative hyphæ, was mounted as a hanging drop culture and the subsequent development followed under the microscope. After growing vegetatively for a time apical growth in the hyphæ becomes arrested by the formation of terminal sporocysts. All details in connection with the formation of these sporocysts agree exactly with the account already given as typical for the group. The discharge is apical, the zoospores are motile at the time of discharge and show encystment after a period of active swarming (Pl. 1, Figs. 1—4). The first motile stage was found to last for a period varying from five to ten minutes. After encystment the spores rested for a much longer period. The shortest resting period observed was six hours. The more usual time appeared to be from twelve to eighteen hours. At the end of the resting stage the zoospore within the wall of the cyst protrudes as a small bud (Figs. 5—7); this bud increases in size and soon a line of separation can be seen between the zoospore and the inner side of the wall. The whole body of the zoospore is very contractile and has to squeeze through the very small opening in the cyst wall. This whole process was found in a great number of cases to take just one minute, that is from the appearance of the small bud to the time when the zoospore had completely discharged. The zoospore now remains attached to its empty case for a period varying from four to ten minutes, or in some cases half-an-hour. Just after leaving the case the zoospore is nearly spherical in form, the first change noticed is a slight elongation in a direction tangential to the empty cyst. A contractile vacuole appears, and the cilia are seen as outgrowths, but their point of attachment is very indefinite, as they seem to wrap themselves round the spore and keep up continuous undulating movements. Their growth in length and the increase in rapidity of their motions is distinctly noticeable. When the cilia have developed to a certain length, their motion in the liquid medium causes the whole zoospore to rock, while attached to the empty case. As the cilia attain their full size the rocking motion increases, and suddenly the zoospore becomes detached, and swims rapidly away. The second motile stage lasts much longer than the first—usually from twelve to twenty-four hours. The spores then come to rest, and develop a cell wall, and usually commence to germinate directly by putting out a germ tube, which, in a suitable medium, can produce a new mycelium.

A difference in the forms of the two kinds of zoospores was noticed and also the motion in the water appears different—that of the second form being much more active. The following method was used for examining them in detail. A hanging drop culture which was seen to possess many zoospores was taken and from this some of the water was removed with a platinum loop to a clean slide, a small drop of water was added and the whole slide then inverted over strong glacial acetic acid for thirty seconds. A trace of chlor-zinc-iodine was added and a cover-glass placed on the drop. This method stains the cilia well; the point of attachment can be seen to be terminal in zoospores discharged from the sporocyst (Fig. 34), but in the case of those of the second motile stage the point of attachment is very difficult to make out. In many cases in the second stage a difference in length between the cilia was apparent, whereas in those of the first stage the cilia are equal in length. The zoospores of the second stage (Fig. 35) seem to be less sharply pointed than those of the first and to have a clear central vacuole as distinct from the smaller apical vacuoles of the zoospores of the first stage.

After discharge of the zoospores, the end of the hypha was often observed growing through into the empty sporocyst (Fig. 8), where a new sporocyst would be formed. All the details so far described are typical of the genus *Saprolegnia*.

The two commonest variations of this life cycle were the formation of gemmæ or resting sporocysts and multiple sporocysts. The first variation is common to several species and genera and should perhaps be counted as part of the general life cycle.

(2). *Gemmæ* resemble the early stages of sporocysts before the cleavage furrows are formed, so far as their internal structure is concerned, but they differ in shape, being usually much shorter and having an oval outline (Fig. 15). They all show a central cavity or vacuole within a peripheral layer of granular protoplasm. The gemmæ can rest in this condition for an indefinite period. In old cultures they easily become detached from the hyphæ (Fig. 16) and can be found in great numbers in the liquid medium. This property affords one method of obtaining pure cultures, as gemmæ can be separated and transferred to sterile plates of media in Petri dishes by means of a small pipette or a platinum loop.

The subsequent development of the gemmæ depends to a great extent upon the medium. If they are transferred to a rich food medium, such as beef extract, they invariably develop at once vegetatively (Figs. 17, 18), producing outgrowths from one or more points on their surface. Usually the germ tube is produced from one end of the gemma, and, branching freely, forms the new mycelium. If, however, the gemmæ, are transferred from an old culture fluid to hanging drops of distilled water, most of them develop into sporocysts and discharge motile zoospores (Figs. 21-23).

The shape of these sporocysts is rather different from those formed normally in the mycelium. The normal sporocyst has a very short process developed at discharge, while the sporocysts developed from gemmæ develop a very long tubular process, which, in some cases, is so very long as to render the discharge of the spores very difficult. Many spores consequently remain within the sporocyst, where they may be seen germinating.

Most writers describe "gemmæ" and "resting sporocysts" as identical, but although transitional stages can be found, the typical gemma can be distinguished from the typical resting sporocyst, as found in the cultures used in this laboratory. After examining numerous cases the following distinction could be drawn.

(2A). *The true gemma* is formed terminally on a hypha, and consists of a single cell, oval in outline, with a continuous cell-wall. When mature it is easily separated from the hypha. Some forms are more elongated and have one or more dense protoplasmic septa. The normal method of germination, when placed in new food material, is as a vegetative bud.

(2B). *The true "resting sporocyst"* is also borne terminally on a hypha and usually consists of more than one cell (Figs. 13, 14), in some cases of a whole chain of cells—in old cultures as many as ten cells have been found in a chain (Figs. 11, 12). It does not separate easily from the hypha. The normal method of development when placed in a new food medium, is to develop into sporocysts and to discharge zoospores in basipetal succession.

(3). *Multiple sporocysts*, referred to by several authors, were always formed in old cultures, and developed first as resting sporocysts, no discharge taking place till they were transferred to a new liquid medium (Figs. 13, 14).

(4). *Chlamydospores* were found on a culture on a fly in hæmoglobin and peptone solution, made up according to Kauffman's formula. They closely resembled gemmæ in appearance, and many were found detached from the hyphæ. On germination they produced a short filament terminating in a sporocyst discharging motile zoospores (Figs. 19, 20). Some cases were observed where a secondary gemma was found in place of the sporocyst.

The cases so far described, (2A), (2B), (3) and (4), merely indicate various phases in the life-history of a genus. They do not show any generic differences. The other cases now to be described all show some modification of the sporocyst and method of discharge or germination, characteristic of the various genera. All the cases were observed in hanging drop cultures on various media made from the stock pure culture.

(5). *Leptomitus-type of sporocyst.* On a two days' old hanging drop culture on the skin of fish in distilled water, two forms of sporocyst were found on the same mycelium. The first form was the ordinary *Saprolegnia*-type (Figs. 1, 2), the other form was a very long slender sporocyst (Figs. 24, 25), with a single row of zoospores, the method of discharge being either terminal or lateral. The shape of the sporocyst and the formation of the zoospores in a single row closely resemble the normal form of the genus *Leptomitus*.

(6). *Pythiopsis-type of sporocyst.* In a hanging drop culture in leucin solution with mycelium taken from the skin of fish, the shape of the sporocyst was that typical of *Saprolegnia*, the discharge of several was observed and seen to consist of motile zoospores, the swarming was very feeble and all spores came to rest quite near the sporocyst (Fig. 26). As very few spores were formed the position of each was carefully noted and the slide was kept under the microscope for observation. After five hours the spores were all found to have germinated directly in the same position (Fig. 29). No signs of any empty cases were found in the culture so that it was concluded that either the second motile stage had been suppressed, or that the zoospores had been discharged in the second motile stage—in the latter case they show the characteristic feature of the genus *Pythiopsis*.

(7). *Achlya-type*. In shape the actual sporocyst resembles that of *Saprolegnia*, but it differs in the manner in which its spores are discharged. Many cases were found where the spores collected into an irregular mass at the mouth of the sporocyst (Fig. 28), in which position encystment took place, and after the usual period of rest, the zoospores emerged from the cyst-wall, and entered upon the second motile stage, which is really the only " motile " stage in this genus, as although the zoospores on discharge have cilia, they only swarm to the mouth of the sporocyst. Resemblance to the genus *Achlya* was also seen in the method of branching of the sporocyst (Figs. 9 and 16), and in the formation of new sporocysts as lateral branches from the base of the old sporocyst. These conditions were found in a twelve days' old culture, on the skin of fish in water, where they seemed to be the normal method. The same conditions have been found from time to time on various hanging drop cultures.

(8). *Dictyuchus-type*. In a hanging drop culture in water taken from a nine days' old culture on white of egg, the numerous resting sporocysts present on the mycelium commenced to develop into sporocysts. In by far the greater number of cases observed, the spores encysted within the sporocyst before its discharge, in spite of the fact that a tubular process was developed on the sporocyst before the spores encysted (Figs. 30, 31). The zoospores were observed leaving the cyst-walls and escaping through the tubular process, pushing before them the empty cases which were in the tube. The property of encysting within the sporocyst is characteristic of the genus *Dictyuchus*. This condition was frequently produced when resting sporocysts on an old culture on egg, were transferred to water-cultures.

9. *Aplanes-type.* In a hanging drop culture two days old on the skin of fish in water, small sporocysts were observed at the ends of hyphæ which seemed to be normal in appearance. They were kept under observation, to watch the discharge of spores, but in this case it never took place. They seemed quite ready, but no motion of the spores could be seen within the sporocyst and each appeared very clearly defined and spherical (Fig. 33). The slide was kept under the microscope till next morning, when the spores were found to have germinated directly while still in the sporocyst, so that the spores had never passed through any motile stage (Fig. 32). This feature is characteristic of the genus *Aplanes.* On the same culture sporocysts were observed discharging motile zoospores in the normal manner.

Although all the conditions found in these investigations may be directly due to the method of culture or to the sudden change from one medium to another, it shows how very variable this species is and how easily it can alter the form and method of discharge of the sporocyst. It is moreover a remarkable fact that the characteristics of six genera can be obtained from one pure stock culture. The results have been so very variable on several points that it is almost impossible to say whether this species should be attributed to the genus *Saprolegnia* or to *Achlya.* The following characters common to these two genera have been observed in the present species:—(*a*) discharge of motile zoospores; (*b*) encystment of zoospores; (*c*) second motile stage; (*d*) formation of gemmæ; (*e*) formation of multiple sporocysts; (*f*) formation of dictyo-sporocysts.

On the assumption that the first-formed sporocyst on a new mycelium will be more likely to represent the typical form for the species, the balance is in favour of the genus *Saprolegnia*, as the first-formed sporocysts were nearly always found to discharge actively motile zoospores which showed a definite swarm-period lasting for several minutes.

In spite of the trial of a great variety of media and of the various culture solutions recommended by Kauffman as being a means of inducing the formation of sexual organs, no signs of the formation of any form of sexual organs has so far been found—that is during a period of culture extending over four months.

The general routine of any culture is as follows:—After inoculation, a mycelium is formed and grows rapidly, forming a fringe around the medium. Sporocysts are formed after thirty-six hours, and continue to be formed till the third or fourth day in increasing proportions; after the fourth day resting sporocysts or gemmæ are formed, and by the ninth day the mycelium is found to be thickly covered with these and all growth seems to have stopped. In this condition the mycelium can remain for an indefinite period. On transferring some of the mycelium bearing resting sporocysts and gemmæ to a fresh medium, these germinate in the manner already described and so the life-cycle can be repeated.

Sporocysts seem only able to be formed as long as the medium in which the mycelium is growing is fresh; as soon as it has been in the same medium for a few days, the formation of sporocysts is inhibited, yet if the mycelium is transferred to another Petri dish with the same medium, but in which there has been no previous growth, the formation of sporocysts continues for a further period of about three days, and then stops again.

One other phenomenon is frequently exhibited in cultures where numerous zoospores are present, and apparently comes into play at the close of the second motile stage. This is "adelphotaxy," or the mutual attraction of zoospores at close quarters The zoospores are very numerous in these cultures, and are necessarily brought into close contact while swarming in a small drop of water. As their motions become less active, the attraction they exhibit for one another becomes more marked, and they are frequently found collected together into a mass, in which state they germinate and form the new mycelium (Fig. 29).

SUMMARY.

As the result of keeping a species of *Saprolegnia* under observation for a period of five months, it has been found possible to obtain on the same mycelium the methods of asexual reproduction which are characteristic of six different genera, viz:—*Saprolegnia*, *Achlya*, *Leptomitus*, *Pythiopsis*, *Dictyuchus* and *Aplanes*.

It is believed that, although previous observers have thrown doubt on the validity of this classification as a result of their observations on the sporocysts of different genera, this is the first time that the characters of so many genera have been obtained from one species.

Full details of the methods of culture by which these various forms were obtained are given in the body of the paper, together with a full analysis of the genera based upon the methods of asexual reproduction that previous workers have established.

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June, 1910.

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For explanations of the Figures on Plates I. and II. see the text.

THE LEAF OF *COLLIQUAYA ODORIFERA*, MOLIN.

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[With Text-Figs. 19—25.]

COLLIQUAYA ODORIFERA is a component of the bushy sclerophyllous woodland which occurs on the slopes of the Chilian Andes at heights between one and two thousand feet. An account of the anatomy of the tribe Hippomaneæ of the Euphorbiaceæ is given in an inaugural dissertation for the degree of doctor, accepted by the Faculty of Philosophy in Munich in 1897. The author, Herbert, describes the leaf and axis of *C. odorifera*, but his descriptions were, as he says, based upon the examination of herbarium material to which he had access. The leaf is large and ovate with a serrate margin, having at the apex of each tooth a prominent, black, almost spherical "gland." These glands, which form the most characteristic feature of the leaf, are neither mentioned by Herbert in his dissertation, nor by Solereder in his Systematic Anatomy of the Dicotyledons (English Edition, 1908). It should be mentioned, however, that the latter author relies to a considerable extent on the former for information as to the anatomy of the Hippomaneæ.

While investigating the structure of these glands the writer made an examination of the other portions of the leaf of *C. odorifera*, and as his conclusions did not agree in all respects with those of Herbert it seemed advisable to publish them.

The material investigated was taken from a plant, raised in a greenhouse by Mr. G. F. Scott-Elliott from seed collected by that gentleman in Chili. A large well-grown twig which was preserved in spirit was used. This twig contained several large full-grown leaves together with numerous smaller ones. Microtome sections of most of these leaves were cut and the following description is based on them.

Epidermis.—There is very little difference between the cells of the upper epidermis and those of the lower in shape, size or thickness of cuticle. The former, are, however, not uniform, being larger near the base of the leaf and also near the middle. Over the median nerve they lose their typical structure and become collenchymatous. These collenchymatous epidermal cells overlie a bundle of collenchyma, roughly triangular in section, which forms a more or less prominent ridge, overlying, and parallel to, the median nerve (Fig. 24). Stomata occur on both surfaces, but they are more numerous and strongly developed on the upper one. The guard-cells are strongly thickened and slightly sunken (Fig. 20). Subsidiary cells, which are parallel to the guard cells, are present, the most common arrangement being that shown in Fig. 19, where there are two subsidiary cells on one side of the pore and one on the other. Sometimes a pair of subsidiary cells occurs on each side.

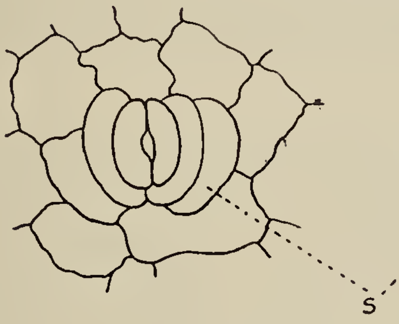

Fig. 19.

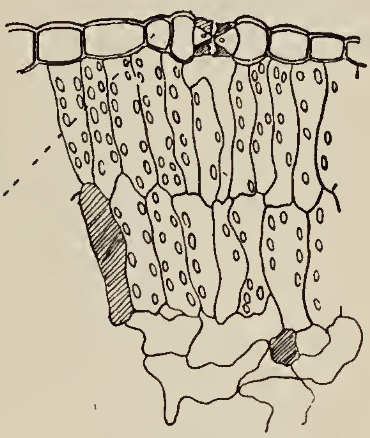

Fig. 20.

Fig. 19. Surface view of a stoma with subsidiary cells.

Fig. 20. Palisade-layer midway between median nerve and margin.

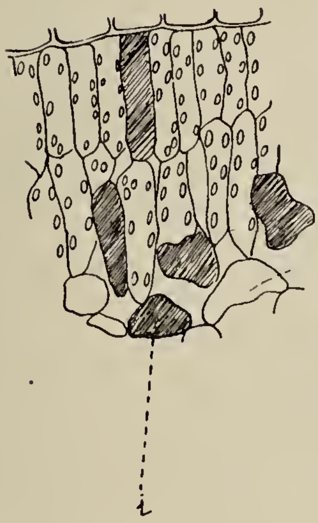

Fig. 21.

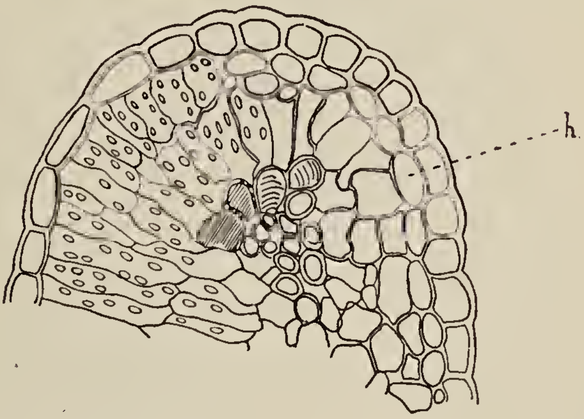

Fig. 22.

Fig. 21. Palisade-layer nearer the margin with secretory cells.

Fig. 22. Transverse section of the marginal portion of a mature leaf. h., hypoderm.

Vascular Tissue.—The nerves are much branched and the ultimate branches anastomose freely. The xylem of the main nerves is strongly developed and consists for the most part of large pitted elements. The medullary rays contain secretory cells, while idioblasts with mucilage occur in the bast. Surrounding the median nerve is a ring of collenchyma composed of small elements. This becomes discontinuous near the leaf-base and forms there two isolated patches (Fig. 24). In this region latex tubes,—the "ungegliederte Milchröhren" of Pax, are found in large numbers. Between the xylem and the collenchymatous sheath isolated strands of wood-parenchyma pass. These are three in number near the base, but die out near the apex.

Ground-Tissue.—The palisade-tissue is two-layered and composed of large cells. The arrangement of these is quite regular, until they pass into those forming the middle collenchymatous patch. Here they become somewhat irregular (Fig. 24). Under the stomata schizogenous intercellular spaces are found between two previously contiguous palisade-cells. ; Some of these cells assume a secretory function, especially near the leaf-margin (Fig. 21), where the palisade-layer passes into a definite hypoderm one cell in thickness (Fig. 22). This was not noticed by Herbert. probably because of the nature of the material examined. The spongy tissue

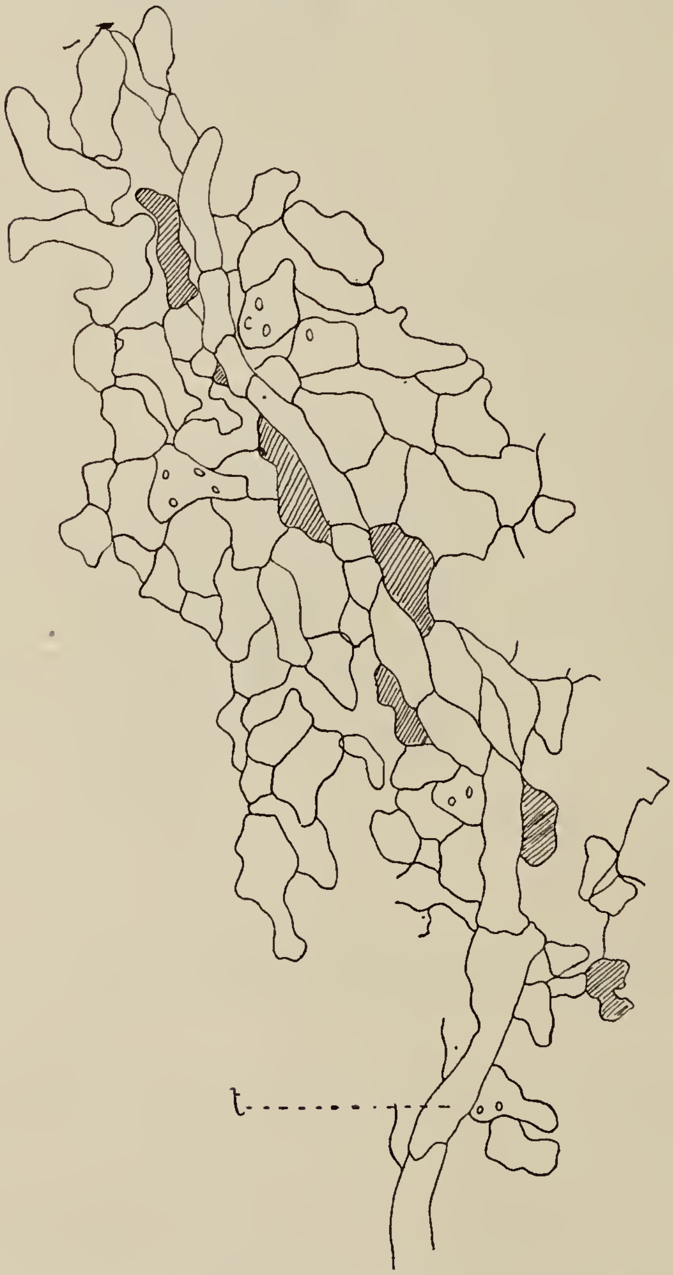

Fig. 23. Series of elongated cells in mesophyll with associated secretory cells.

is very lax and is composed of ordinary and secretory cells in approximately equal numbers. The secretory elements here are of two kinds, ordinary cells which have assumed the secretory function, and idioblasts with denser darker-coloured contents. In association with these long series of cells sometimes occur (Fig. 23).

Glandular Structures.—These are found on the leaf-teeth and form the most prominent and characteristic feature of the leaf.

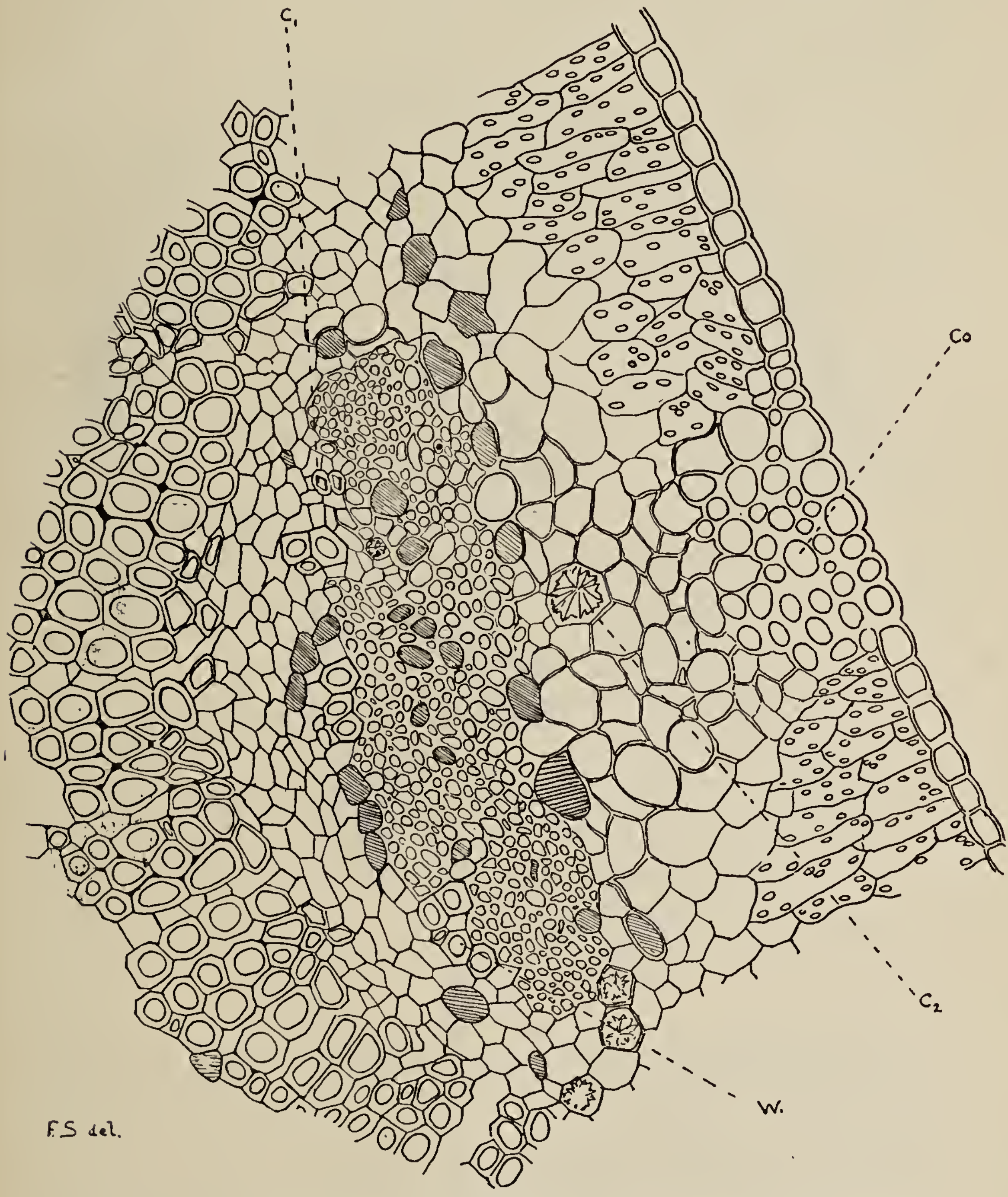

Fig. 24. Portion of transverse section of midrib of leaf taken near the base. C_0, collenchyma; C_1, single crystal; C_2, aggregated crystals; W, wood-parenchyma.

Externally they appear as large black caps covering the tips of the teeth. In sections taken parallel to the plane of the leaf their peculiar structure can be well made out. They are irregular in shape, being composed of a mass of latex which has hardened on exposure to the atmosphere. In this mass are embedded the remains of the hypodermal and epidermal layers, ruptured when the latex exudes in the first period of activity of the glands. A vascular bundle traverses each glandular structure, terminating in a few groups of large spiral tracheids (Fig. 25). Into the base of the structure the secretion is poured, the secretory elements being in intimate association with the vascular bundles.

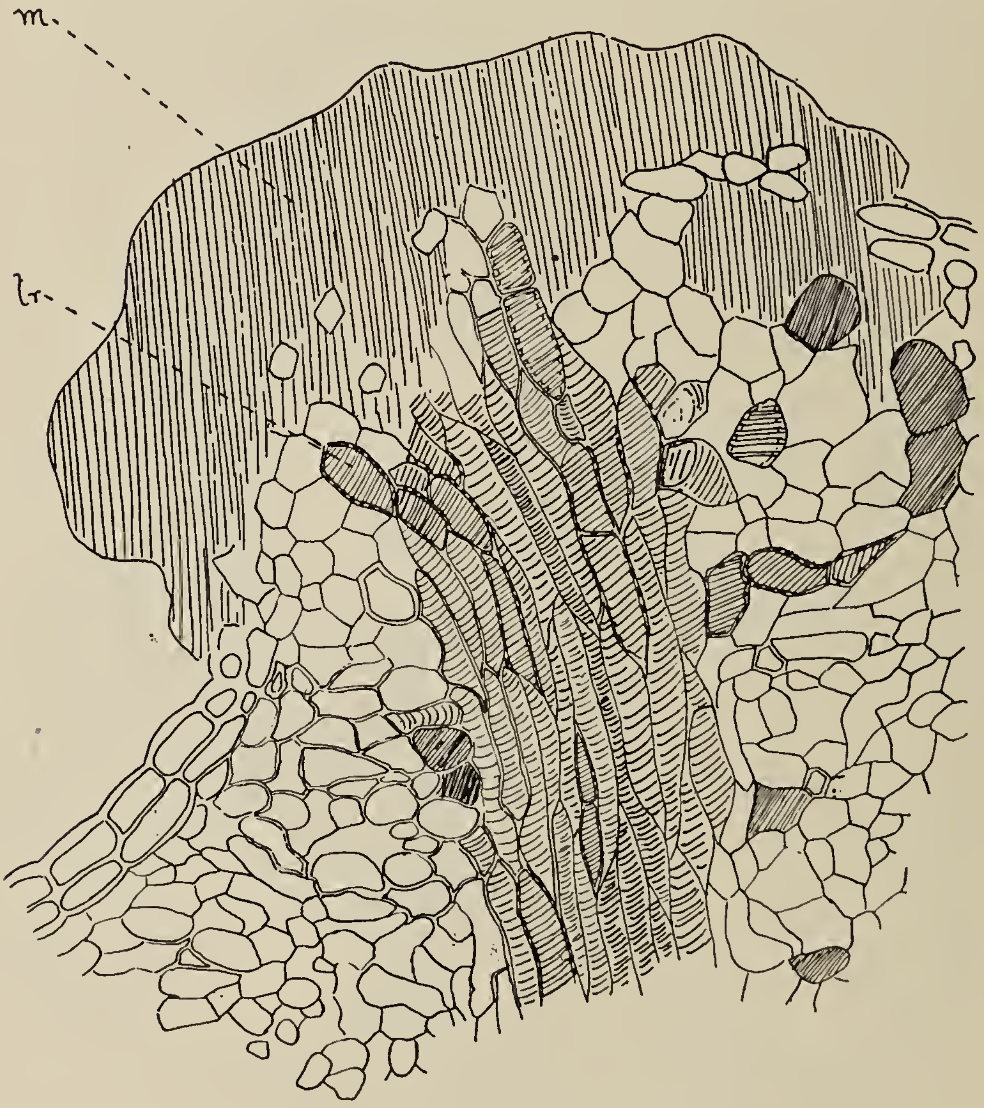

Fig. 25. Section through a leaf-tooth, parallel to the plane of the leaf, m., hardened mass of secretion; tr. terminal tracheids.

Calcium oxalate is present in the cells of the bast and mesophyll, in the form of single or aggregated crystals.

Tannin is present in considerable quantity. It was not possible to localize the secretion by means of micro-chemical tests, as the whole of the cells had become impregnated with it.

SUMMARY.

In connection with the anatomy of the Euphorbiaceæ the following points in the structure of the leaf of *Colliquaya odorifera*, Molin. appear worthy of notice.

1. The occurrence of large glandular structures on the leaf-teeth. These retain their functional activity until the leaf is mature.
2. The leaf is bifacial with a two-layered palisade region on the upper side, not centric with a three-layered palisade region on both sides as Herbert reports.
3. A definite hypoderm is present near the leaf-margin. Herbert found hypoderm among the Hippomaneæ only in species of *Gelonium* and *Excœcaria*.
4. The chief development of stomata is on the upper surface.
5. The occurrence of three kinds of secretory element. (*a*.) Latex tubes (ungegliederte Milchröhren). (*b*.) Idioblasts with latex. (*c*.) Ordinary cells of the palisade-tissue and spongy-tissue which perform the secretory function.

I am indebted to Mr. F. J. Lewis, M.Sc., F.L.S., for the material, and also for kind suggestions and criticisms.

NOTE ON CERTAIN INTUMESCENCES IN ROOTS.

IT has often been shown that, in the case of injury to the epidermal tissues of shoots, the cortical cells underlying the wound elongate towards it. Also, intumescences in leaves are regarded as a wound response (Cf. Dale, Phil. Trans. B Vol. 198, p. 221 and the literature there quoted). Experiments show that a similar reaction occurs in the cortical cells of roots.

Dr. Bayliss recorded abnormally elongated cortical cells (Bayliss, Annals of Botany, Vol. XXI, p. 397), in investigating the galvanotropism of roots. At the suggestion of the late Professor Hillhouse, an attempt was made to determine the nature of the response—whether it was due to electrical or traumatic stimulation.

The primary roots of seedlings were injured in the following ways:—(i) an electric current of the order of a milliampère was passed through roots by direct contact of platinum electrodes; (ii) an electric current was passed through soil in which seedlings were growing; (iii) a spark from a coil passed through the roots; (iv) by local application of acid, and of alkali; and, (v) by branding with a hot glass rod.

In all cases the seedlings were allowed to continue growth in sawdust, after the production of the injury, for periods ranging from one to fifteen days. Sections showed that where the epidermal cells had been destroyed (no matter what the agent) and a scar had formed, the uninjured cortical cells below the scar had elongated towards it. The length of the hypertrophied cells was found to be dependent on the time allowed for their growth.

In the experiments where roots were growing in a soil through which a current was passing (about a milliampère) there were no intumescences produced. This is probably due to the fact that the current did not pass through the roots, since they offer a greater resistance than a moist soil. Consequently there were no sudden chemical or thermal changes in the root and no wound. Therefore, there is no reason to believe that the electrical stimulation acts in any other way than as a traumatic stimulus.

These intumescences resemble those in shoots in that they are produced in tissues which are normally quiescent, there is no active growth by cell-division, but an enlargement of previously full grown cells accompanied by amitotic nuclear division.

The conclusions to be drawn are:—(i.) that the elongation of the cells is not due to electrical stimulus as such, and (ii.) that the growth in length is a traumatic response comparable to intumescences in shoots.

CREWE, H. V. DAVIS.
May 11th, 1910.

THE BRITISH ASSOCIATION AT SHEFFIELD.

THE British Association Meeting at Sheffield (August 31st to September 7th) was distinctly a good one. In particular the local arrangements were excellently carried out, practically indeed without a hitch. This is no mean achievement nowadays, when the Association makes greater demands on the local resources than ever before. In fact, the growth of the Association has introduced new and difficult problems, the solution of which may possibly result in some radical changes of policy within the next few years. The formation of each new section renders it increasingly difficult for any but the largest towns to accommodate the Association, and indeed one even hears the opinion voiced occasionally that the Association itself might well be replaced by entirely independent meetings of its various sections. The Council apparently favours a general policy of convergence, endeavouring to encourage joint meetings between different sections, and to discourage the multiplication of sections. In fact, there are some who advocate the actual amalgamation of sections already formed. But however desirable such amalgamation might be on administrative grounds, it can scarcely be denied that the subdivisions already made have been the unavoidable outcome of the perfectly natural and healthy progress of science itself. That being so, and while properly organised joint meetings have considerable value, any attempt to interfere seriously with natural developments, and to bring about artificial unions, could only be regarded as a retrograde step. However, time may be entrusted with the solution of these wider problems; meanwhile we are more nearly concerned with the proceedings of Section K at the Sheffield meeting.

Although the total number of members present at Sheffield was below the average, the attendance in Section K was the best for some years, a marked feature being the presence of a large contingent of the younger men. The section warmed up as the meeting proceeded; indeed, although afternoon sessions were the exception rather than the rule, on one occasion it enthusiastically discussed papers of a morphological nature till after 5.30 p.m.

The President's Address.

Selecting for his subject the development of systematic field botany, Professor J. W. H. Trail delivered his Presidential address (which was one of the shortest on record) on Thursday morning, September 1st. The address is particularly opportune at the present time, when, owing to the work not only of systematists, but also of ecologists, renewed interest, and on wider lines than before, is being exhibited in the study of plants in the field. The President passed in review the various floras that have appeared from time to time, and pointed out that a mass of additional data has already been accumulated, but is, at present, to a large extent buried in various scientific journals and the transactions of societies. Hitherto the work has been largely individual, and so far at least as Botany is concerned, there is a conspicuous absence in Britain of more elaborate combined efforts such as are not infrequent on the Continent. Professor Trail put forward a plea for the preparation of a great National Flora. " Such a flora " said he " would probably require to be in the form of monographs by specialists, issued as each could be prepared, but as part of a well-planned whole. It should give for each plant far more than is contained in even the best of our existing British floras. Means of identification must be provided in the descriptions, with emphasised diagnostic characters; but there should also be the necessary synonomy, a summary of topographical distribution, notes of man's influence on distribution, abundance, &c., on any biological or other point of interest in structure or relations to habitat, &c. Local names, uses and folklore should also be included. In a national flora there should be included an account of the successive floras of former periods, and, as far as possible, the changes that can be traced in the existing flora from its earliest records to the time of issue should be recorded." Though it may be long before such a scheme can arrive at fruition, it is certainly one which should command the sympathies and co-operation of a large number of workers. Could the plan be once seriously formulated, it would serve to give point and direction to a great deal of work which is being carried on all over the country, even at the present time. At the President's request, a British Association Committee was appointed to consider and report on the question of the preparation of materials for such a flora of the British Isles.

JOINT MEETINGS.

Monday morning was devoted to a joint meeting with the Sections of Chemistry and Physiology for the consideration of the Biochemistry of Respiration.

The meeting was opened by Dr. F. F. Blackman, who gave a very complete summary of the present state of knowledge and speculation on this difficult subject. He dealt with the matter in three main sections:— (1) the nature of the reaction (or complex of reactions) that constitutes respiration, (2) the extent to which the reaction in the cell conforms to the laws of general chemistry and (3) the influence upon the progress of the reaction of the special medium (protoplasm) in which it takes place. Dr. Blackman described some experiments on the effect of starvation which pointed to the view that the respiratory output of CO_2 has a double origin, partly "protoplasmic" and partly the result of oxidation of "floating" sugar supplies.

The next communication was from Mr. H. M. Vernon, who gave a summary of the possibilities of direct oxidative breakdown of sugars and organic acids in animal tissues and mentioned some of his own experiments on the respiration of excised organs of warm-blooded animals.

Dr. E. F. Armstrong then spoke about the action of oxidases and the strong evidence that some of them are not strictly enzymes at all. He showed the oxidative blackening which results when *Aucuba* leaves are exposed to chloroform, toluene and similar vapours, and he attributed this effect primarily to these vapours being able to pass the semi-permeable protoplasm and set up osmotic disturbances in the cell. He suggested that the blackening would be accompanied by the absorption of oxygen, and the paper that followed by Mr. D. Thoday contained proof that this was so. Mr. Thoday dealt with the stimulation of respiration by chloroform, and described careful experiments shewing to what extent it affects both the intake of oxygen and the output of CO_2. It seemed probable that the chloroform acts by altering the permeability of the protoplasm.

Finally, Professor H. E. Armstrong spoke about the great complexity of oxidation in living cells. He held that organic acids constituted more important stages in the process than was generally believed.

Another joint meeting (with the Zoologists) was held on Friday, when two cytological papers were read before the combined sections. In a paper entitled "The New Force, Mitokinetism," Professor Marcus Hartog gave an account of his theories with respect to the forces at work during nuclear division. As his views have been already published, it will suffice to say here that Professor

Hartog is of opinion that the formation of the spindle in karyokinesis is due, not to magnetism or any other previously recognised force, but to the action of a hitherto undiscovered force, which he terms Mitokinetism. This force, says Professor Hartog, has not been met with so far outside the living cell.

The second paper was by Dr. E. Hindle, on "A Cytological Study of Artificial Parthenogenesis." Ripe eggs were made to undergo artificial chemical fertilisation, and free swimming larvæ were produced, indistinguishable in form and behaviour from those developed from normally fertilised eggs. The cytological changes undergone were carefully described, but unfortunately, owing to the author's slides having gone astray, the descriptions were less easy to follow than would have been the case had the paper been illustrated. Dr. Hindle concluded his paper with the suggestion that the known facts of artificial parthenogenesis may perhaps be competent to explain the origin of cancer.

INDIVIDUAL PAPERS.

As these papers have been already noticed individually in *Nature* (Nov. 10th, p. 58), it is scarcely necessary in this article to do more than indicate in a general way the topics discussed during the various sittings; the papers themselves may be dealt with very briefly. The papers were as usual grouped as far as possible according to their topics. Physiology, morphology and cytology were the subjects most in evidence this year. Fungi also came in for a fair share of attention.

On Thursday morning, in addition to the Presidential Address, various mycological papers were taken. Professor A. H. R. Buller opened the proceedings with a well illustrated paper dealing with "The function and fate of the cystidia of *Coprinus atramentarius*." The author supports Brefeld's view that the cystidia act as props to keep the gills apart. Mr. A. E. Lechmere, in a paper on "Asexual Reproduction in a Species of *Saprolegnia*[1]," stated that in one undetermined species he had found methods of asexual reproduction which had hitherto been regarded as characteristic of six different genera of the family. Professor V. H. Blackman described "Pseudomitosis in Coleosporium." This is a form of nuclear division intermediate between mitosis and amitosis. A spindle, with polar radiations, &c., and a spireme are formed, but the chromatin is distributed to

[1] See the present number of this journal.

the poles without the formation of chromosomes. Mr. Harold Wager discussed "Chromosome Reduction in the Hymenomycetes." In this group reduction is effected by the distribution of the chromosomes in a manner which apparently corresponds to the brachymeiotic phase in the ascus as described by Miss Fraser. Mr. F. T. Brooks gave the results of some preliminary observations and experiments on the "Silver-leaf disease of fruit trees."

Friday morning was occupied in part by the joint meeting with Section D already referred to, and in part by other papers dealing with cytology and also with heredity. Miss Fraser and Mr. J. Snell contributed a paper on "Vegetative Mitosis in the Bean," and Professor J. B. Farmer and Miss Digby one "On the Somatic and Heterotypic Mitoses in *Galtonia*." In these two papers the respective authors agreed in stating that the longitudinal fission which occurs during mitosis is initiated during the telophase of the preceding division. Professor V. H. Blackman produced circumstantial evidence that "the vermiform male nuclei of *Lilium*," though devoid of cilia, are in reality capable of movement.

Professor F. E. Weiss, in an account of "Colour-inheritance in *Anagallis arvensis*," showed that in this case red is dominant and blue recessive. Mr. R. P. Gregory gave some "Further Observations on Inheritance in *Primula sinensis*."

Professor F. O. Bower gave the semi-popular lecture on Friday afternoon, his subject being "Sand-dunes and Golf-links."

Monday afternoon was devoted to anatomical and other papers. Professor Bower began with a brief "Note on *Ophioglossum palmatum*," bringing forward anatomical evidence that this species, like *O. pendulum* and *O. simplex*, is an extreme and specialised type. The same author also contributed a paper "On two Synthetic Genera of Filicales." The two genera in question are *Plagiogyria* and *Lophosoria*, both of which the author regards as having arisen from types related to the Schizæaceæ and Gleicheniaceæ. From this starting-point Professor Bower traced two parallel sequences of living forms, passing respectively through these genera, and leading in one case to the Pterideæ, and in the other to the Cyatheaceæ. Dr. Kidston and Professor Gwynne-Vaughan in a paper "On the Fossil Genus *Tempskya*," suggested that the extraordinary "false stems" of this fossil may throw light on the evolution of the erect arboreal stems of modern tree-ferns. Miss M. C. Stopes gave some "Further Observations on the Fossil Flower," dealing particularly with the structure of the ovary wall. Mrs. Thoday discussed "The Morphology of the Ovule of *Gnetum africanum*," and concluded that it is more primitive than that of *Welwitschia*. Professor F. W. Oliver next gave a paper "On the Diversity of Structures termed Pollen-Chambers," in which he showed that several of the lesser known fossil seeds possessed a nucellar apex of a much more complex character than that found in *Lagenostoma* or *Physostoma*. The author suggested some interesting comparisons between these seeds and those of some of the Medullosæ and also *Ginkgo* and Cycads. A lengthy but very interesting afternoon session concluded with a paper "On the Stock of *Isoëtes*" by Professor W. H. Lang. Dr. Lang's explanation of the downwardly growing root-bearing region, with its depressed and hidden apex, was thoroughly convincing. It throws welcome light on an obscure morphological problem.

On Tuesday morning a number of physiological papers were read. Mr. S. Mangham gave an account of some experiments he made in order to determine "The Paths of Translocation of Sugars from Green Leaves." His results furnish positive experimental proof of Czapek's belief that the sieve-tubes alone are responsible for rapid translocation over long distances. Mr. D. Thoday next discussed "Assimilation and Translocation Under Natural Conditions," dealing particularly with increases in dry weight of both attached and detached leaves under varying experimental conditions. Mr. A. S. Horne read a paper on "The Absorption of Water by Certaln Leguminous Seeds." The author dealt with the swelling of these seeds under different conditions, in the light of a knowledge of their anatomy.

On Wednesday morning Professor Bottomley gave an account of some observations on "The Association of certain Endophytic Cyanophyceæ and Nitrogen-fixing Bacteria." The Cyanophyceæ in the leaves of *Azolla* and the thallus of *Anthoceros* appear to be always associated with *Azotobacter* and *Pseudomonas*. The author suggested that the association of the Algæ and Bacteria may be a symbiotic one. Mr. J. H. Priestley gave some "Notes on the Distribution of Halophytes on the Severn Shore," and discussed the general adaptation of the plants of the pelophilous zones to their habitat. The last paper was by Mr. M. Wilson, on "Plant Distribution in the Woods of North-east Kent. Mr. Wilson concluded that the most important factor in this distribution is the character of the soil.

Excursions, &c.

The only special botanical excursion arranged was held on Saturday, September 3rd, when a large number of botanists spent the day in Derbyshire; visiting Grindleford, Stoney Middleton, Eyam, &c., under the guidance of Mr. Snelgrove. The day was a fine one, and everyone seemed to enjoy the relaxation from the more serious business of sectional meetings. The special botanical objective was the examination of the millstone grit and mountain limestone floras.

Mr. Doncaster kindly invited the Zoological and Botanical members of the Association to a garden party on Tuesday afternoon. Unfortunately a number of members had left by this time, but those who were able to accept the invitation were delighted with Mr. Doncaster's charmingly laid out grounds.

Section K was fortunate in securing the services of Mr. B. H. Bentley as local secretary. Both he and his Assistant, Mr. A. W. Bartlett contributed greatly to the general success of the meeting.

R.H.Y.

NOTES ON RECENT LITERATURE.

The Cactaceæ, and the Study of Seedlings.

An interesting contribution to our knowledge of seedling anatomy—namely a study of the "transition phenomena" in seedlings of the Cactaceæ—has recently been made by Miss de Fraine.[1] The anatomy of the seedlings of this order has hitherto remained unknown, but this gap in our knowledge has now been very thoroughly filled, since Miss de Fraine has investigated no less than forty-seven species, belonging to eleven genera. The most striking results of her enquiry into the mode of transition from stem- to root-structure may be briefly stated as follows[2]:—

In the group of genera whose seedlings most closely resemble those of ordinary Dicotyledons (*Pereskia*, *Opuntia*, and *Nopalea*) a type of transition is found corresponding to that known as the "*Anemarrhena* type."[3] In those genera, on the other hand, whose seedlings are more profoundly modified, in accordance with the

[1] Ethel de Fraine. "The Seedling Structure of Certain Cactaceæ." Annals of Bot., Vol. XXIV, p. 125, 1910.

[2] Summarised l.c., p. 164.

[3] Ethel Sargant. "The Origin of the Seed-leaf in Monocotyledons." New Phytologist, Vol. I, p. 107, 1902.

xerophytic habit of the mature plant (*Phyllocactus*, *Cereus*, *Echinocactus*, etc.), the transition corresponds to Van Tieghem's third type.[1]

From a theoretical point of view, the discovery of the *Anemarrhena* type of transition among the Cactaceæ is of great interest. It will be recalled that in *Anemarrhena* (a member of the Liliaceæ), there are two bundles in the cotyledon. Passing downwards we find that each phloem group branches into two, while each xylem strand divides into three. The lateral xylem groups unite in pairs, and the result is a tetrarch root-stele. Miss Sargant's examination of about sixty species belonging to the Liliaceæ led her to "regard the *Anemarrhena* type as primitive, and as the starting-point from which most, if not all, the vascular types characteristic of Liliaceous seedlings have been historically derived." [2] She further concludes that this type "may very well be primitive among Monocotyledond in general as well as among the Liliaceæ proper." [3]

A type of transition closely recalling that of *Anemarrhena* has been also observed in *Eranthis*, among the Ranunculaceæ. It will be recalled that this resemblance led Miss Sargant to believe in a real genetic connexion between *Eranthis* and *Anemarrhena*, and to suppose that they are descended from a common ancestor with two seed-leaves, each represented by a single trace in the hypocotyl. Her theory of the origin of Monocotyledons from a dicotyledonous stock, by the fusion of two seed-leaves into one, was largely suggested by the resemblance which exists between the seedling structure of *Eranthis* and *Anemarrhena*. In the former, the petioles of the cotyledons are united into a tube. Some stress is laid on this point, since it was supposed that this particular form of vascular symmetry had something to do with the partial union of the cotyledons in *Eranthis*, and their (theoretical) complete union in *Anemarrhena*.

We may now consider the bearing of Miss de Fraine's discovery of the *Anemarrhena* type of transition among the Cactaceæ, upon the geophilous theory of the origin of Monocotyledons. The view that Miss de Fraine herself takes is that "It cannot be considered that the resemblance of *Opuntia*, for example, to *Anemarrhena* is the result of a close genetic relation between the two; nor can it be conceded that it is due to a response of two unrelated forms to similar conditions; hence we cannot but conclude that the resemblance is accidental."[4] She goes on to point out that, if this is so, there is no reason for regarding the similarity between *Eranthis* and *Anemarrhena* as anything but accidental also. Later on she adds that "the evidence on which the 'fusion' hypothesis was based has been considerably weakened by the discovery of the *Anemarrhena* type in seedlings of such a specialized order as the Cactaceæ."

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[1] Ph. van Tieghem. Traité de Botanique. 2nd French Edn., Paris, 1891, Vol. I, p. 782.

(Van Tieghem's types of transition are also enumerated by Miss Sargant in "A New Type of Transition from Stem to Root in the Vascular System of Seedlings." Annals of Bot., Vol. XIV, p. 634, 1900).

[2] E. Sargant. "A Theory of the Origin of Monocotyledons, founded on the Structure of their Seedlings." Annals of Bot., Vol. XVII, p. 4, 1903.

[3] E. Sargant. "The Reconstruction of a Race of Primitive Angiosperms." Annals of Bot., Vol. XXII, p. 169, 1908.

[4] l.c., p. 167.

It will be admitted that the force of Miss de Fraine's argument depends very largely upon the systematic position to be assigned to the Cactaceæ—a subject which she does not discuss. There can, of course, be no question but that this order is "specialized" as regards its vegetative characters, but it is the reproductive organs, and not the vegetative features of the mature plant, which are of prime importance as regards affinities. As Darwin wrote in the chapter on "Classification" in the Origin of Species,—"With plants how remarkable it is that the organs of vegetation, on which their nutrition and life depend, are of little signification; whereas the organs of reproduction, with their product the seed and embryo, are of paramount importance!"[1]

The Cactaceæ are usually regarded as an isolated group of obscure affinities, and in different systems of classification they occupy very various positions. For instance Engler and Prantl[2] place the Cohort Opuntiales, containing the single order Cactaceæ, between the Parietales and the Myrtifloræ. In Potter's translation of Warming's Systematic Botany,[3] on the other hand, the Cactifloræ (corresponding to Engler's Opuntiales) are placed immediately before the Polycarpicæ (otherwise called Ranales). An examination of the floral characters leads one to suppose that the latter position gives perhaps the best indication of the true affinities of the Cactaceæ. They have a remarkable number of features in common with various members of the Ranalian plexus, especially those which are regarded by some authors as retaining many primitive characters, such as the Nymphæaceæ and Magnoliaceæ. The most striking of these "Ranalian" characters are the following:—The flowers are noticeable for their acyclic structure,—there are numerous spirally arranged sepals, petals and stamens. In certain cases the floral leaves clothe the external surface of the receptacle, and there is a gradual transition between the small sepaloid, and the large brightly coloured petaloid members of the perianth. The carpels may be numerous. As regards the general structure of the flower, a marked similarity may be recognised by comparing the longitudinal sections of such flowers as *Pilocereus* (Cactaceæ)[4] and *Euryale ferox.*[5] (Nymphæaceæ) in both of which the perianth tube is prolonged above the inferior ovary into a tubular structure on the inner side of which the stamens are inserted.

If it is, as the present writer is inclined to think, a justifiable hypothesis that the Cactaceæ are derived from the same ancestral stock as the Nymphæaceæ, and other orders belonging to the Ranalian plexus,—the occurrence of the "*Anemarrhena-Eranthis*"-

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[1] C. Darwin. "Origin of Species," Sixth Edition, p. 343, 1894.

[2] Engler & Prantl. "Pflanzenfamilien." Nachtrag zu Teil II—IV, 1897, p. 352.

[3] "A Handbook of Systematic Botany. E. Warming & M. C. Potter, 1904, p. 375.

[4] Engler & Prantl. "Pflanzenfamilien." III. 6a, p. 180, Fig. 59, 1894.

[5] Engler & Prantl. "Pflanzenfamilien." III. 2, p. 6, Fig. 7F, 1891.

type of seedling structure in this order becomes of greater importance than Miss de Fraine concludes. It is no longer necessary to look upon it as accidental. Among the Cactaceæ this type of transition occurs, as has been already mentioned, in those genera whose seedlings are least modified, and it is in such cases that we should naturally expect to find that ancestral characters had been retained. It would appear that Miss Sargant's view that the various monocotyledonous and dicotyledonous types of seedling anatomy were all originally derived from the *Anemarrhena* type, is strengthened, rather than weakened, by the discovery of this ancestral type among the Cactaceæ.

There is, however, a further question to be considered. How far does the view hold good that, in *Eranthis*, it is the formation of a cotyledonary tube that has led to the survival of the ancestral type of vascular symmetry? It certainly seems as though Miss de Fraine's discovery of the *Anemarrhena* type of transition among Dicotyledons which do not form a cotyledonary tube, tends to disprove this contention. It may well be a mere coincidence that *Eranthis* possesses a cotyledonary tube, while at the same time it has retained the *Anemarrhena* type of vascular symmetry. In discussing this problem it is essential to keep two questions apart in one's mind:—

1. What was the ancestral form of vascular symmetry in Angiospermous seedlings?
2. If it be conceded that the primitive transition structure was of a bisymmetrical type, suggesting a dicotyledonous ancestry,—by what method was the change from two cotyledons to one brought about?

Eranthis happens to supply an answer to each of these questions. It has the bisymmetrical vascular system, and indications of a tetrarch root, which, it may be held, are ancestral. It also possesses fused cotyledons, suggesting a simple way in which one cotyledon can replace two without any loss of symmetry.

As regards seedling study in general, Miss de Fraine closes her paper with the following somewhat pessimistic expression:—"It is not justifiable to use the seedling structure as an indicator or phylogenetic connexions."

Such a statement is difficult to controvert, since no phylogenetic criterion can, in the nature of things, be universal and absolute. The weight to be attached to seedling structure as a clue to phylogeny may be widely different in different families of plants. It is, perhaps, unlikely that a group will ever be discovered in which the seedling structure gives so clear an indication of affinities as it does in the various tribes within the Liliaceæ. This is, however, exactly parallel with other well-known facts, both among plants and animals. Darwin[1] quotes Robert Brown, who says of certain organs in the Proteaceæ, that their generic importance, "like that of all their parts, not only in this, but, as I apprehend, in every natural family, is very unequal, and in some cases seems to be entirely lost." Darwin recalls a similar instance among the Hymenoptera, and concludes, "Any number of instances could be given of the varying importance for classification of the same important organ within the same group of beings."

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[1] L.c., p. 343.

Like all other phylogenetic criteria, seedling structure needs to be used with great caution. If, however, the conclusions drawn from it are constantly checked by appeal to the results obtained in other lines of research, there seems little reason to doubt that it has its value, though this is distinctly greater in some groups than in others.

AGNES ARBER.

THE EFFECT OF HEAT AND ETHER ON THE RESPIRATION AND COMPOSITION OF POTATO TUBERS.

In the current number of *Flora* appears, after an interval of 25 years, a further contribution by Müller-Thurgau to the study of the nature of the resting condition of plants. In his earlier work he investigated the respiration of potato tubers, and the composition of the reserve substances stored in them, at all stages of their life; and he succeeded in constructing from the changes he observed an intelligible picture of their internal organisation under normal conditions. He conceived a balance to exist between the formation of sugars by hydrolysis of starch, and their removal in respiration and by storage as starch again. At the beginning of the resting period the leucoplasts act so vigorously that no free sugar can usually be detected. At 0°C, however, sugar accumulates in considerable quantity, proving that at that temperature starch-formation is largely inhibited, and suggesting that even at ordinary temperatures sugar is still formed, but is completely removed in respiration and starch-formation. As the resting season proceeds sugar begins to appear even at ordinary temperatures; the leucoplasts, becoming less vigorous with age, are no longer able to store again all the sugar which is being formed, and an equlibrium concentration of sugar is maintained at which the rate of sugar-formation (which diminishes with increasing concentration) balances the rate of its removal (which increases with the concentration). This equilibrium concentration rises as the season advances and the vitality of the tuber diminishes.

The respiration is intimately connected throughout with the supply of sugar which is available. It is very high in potatoes which have been kept at 0° and have become sweet: at ordinary temperatures, it is low in the autumn when little or no sugar is present and increases with the accumulation of sugar as the tubers grow older.

In the present contribution the author and a collaborator turn their attention to the nature of the effect which etherisation or temporary exposure to a relatively high temperature produces, in hastening the development of resting organs. Warming has no "forcing" effect on potatoes, but their behaviour is investigated as a preliminary step to the study of other types in which the forcing effect is marked (*e.g.*, *Convallaria* rhizomes). As the work is largely a study in the effect of external conditions, of the nature of stimuli, on respiration, it comes to hand very opportunely at the present time.

The authors find that after exposure to a temperature of 40°C for several hours the respiration at ordinary temperatures is increased; it reaches a maximum intensity about the second day and then slowly falls to the normal intensity. The full effect was found to depend upon a sufficiently long exposure, and not upon the *variation* of the temperature in heating and cooling. With higher temperatures the maximum intensity was higher and was reached rather later; and after exposure to 44° the normal intensity was not regained, but a permanent increase in the rate of respiration resulted.

It is an interesting fact that no stimulation was observed except with temperatures of 38° and over. The effect appears to be such that beyond a certain minimal temperature (37° for one sort of potato) the amount by which the maximum rate of respiration reached by the heated tubers exceeds the rate of respiration of similar unheated tubers is closely proportional to the difference between the temperature used and the minimal temperature, at which the stimulation is zero. Thus after 44° the respiration curve showed a rise $2\frac{1}{3}$ times as great as after 40°. This appears to be true regardless of the original intensity of the respiration which differed considerably in tubers containing different percentages of sugar. (The increase in the total amount of CO_2 evolved, the total amount of "stimulus-CO_2," will of course not be proportional to the rise above the minimum temperature, but will be much greater for each succeeding degree).

From a study of the sugar changes produced, the authors conclude that the fundamental effect of the heating is a weakening of the protoplasm like that ensuing normally as the age of the tuber increases. As a result of this the storage of starch by the leucoplasts, one of the higher protoplasmic activities of the cell, suffers greatly, while at the same time even the lower, enzymic processes, the inversion of cane sugar and the dissolution of starch, are appreciably retarded. Thus at 18°C heated potatoes retain a considerable percentage of sugar in their tissues; while at 0°, at which temperature starch-formation is largely inhibited even in normal potatoes, the slower formation of sugar shows that heating has acted injuriously on that process also, though to a less degree.

The parallel investigation of changes in sugar-content and respiratory activity involved the halving of the tubers, as the only method of ensuring similarity in all respects between control and experimental material. The results were then, however, complicated by the additional reaction to injury. Under these conditions it was found that the two effects were antagonistic. Under the weakening influence of a high temperature, reaction to wounding was at first inhibited, and even after the effect of heating wore off, the respiration never reached the same maximum intensity as was shown by unheated pieces. On the other hand, while unheated injured tuber showed a permanent increase in the rate of respiration, weight for weight, in comparison with whole potatoes, the permanent increase was much greater in the case of the heated tubers.

This permanent increase, observed with whole potatoes also, is attributed by the authors to increased sugar content. In order to feel quite sure that this is a sufficient explanation, one would like to have the results of a series of experiments with different temperatures, corresponding with their series for whole potatoes between 35° and 44°. One would then expect that temperatures which failed to produce a permanent rise in the respiration would also not bring about a rise in the equilibrium concentration of sugar.

The authors have not been able to find any significant differences in the amount of diastase before and after heating, and conclude that the accumulation of sugar after heating does not depend on an increased formation of diastase, but is brought about in the way already indicated.

They also record experiments on the effect of etherisation on halved potato tubers. They found that the maximum in the curve of respiration following the injury by halving was not affected, but was reached rather later (owing to "narcosis" of the protoplasm); the subsequent fall was slower in the etherised potatoes. No alteration of the immediate or subsequent changes of sugar concentration was observed. Etherisation thus differs from heating; it is apparently less drastic. The difficulty of ether penetrating into the interior of the tuber may perhaps account for this; at any rate the "narcosis" suggests comparison with the inhibition produced by heating. Further comparison is not possible as the experiments are very few, and whole potatoes were not used in any of the etherisation experiments.

Further contributions on the same lines will be awaited with interest, and more experiments with the same material would be of value in elucidating the respiratory problems which are involved.

D.T.

PLANT-ANIMALS.

UNDER this title Professor Keeble publishes in the new series of "Cambridge Manuals of Science and Literature" an account[1] of the natural history of those fascinating marine worms *Convoluta roscoffensis* and *C. paradoxa*. Those botanists who are not familiar with Professor Keeble's papers (partly in conjunction with Professor Gamble) on this subject should certainly get and read this little book. And not only for the extraordinary attractiveness of the facts described and the problems involved, which Professor Keeble has largely elucidated in a singularly able and acute manner, but also because the questions raised by these worms are of as much interest to the botanist as to the zoologist, if indeed they are not of even greater importance to the student of plant-life. This study is indeed a real study in biology, the science of life. It has for its object the whole complex of interrelations between a given animal and a given plant, and its problems are some of the fundamental problems of living protoplasm.

The story of how the two species of *Convoluta*, each sharply restricted to a different and perfectly definite zone on the sea-shore, are inhabited, the one by a green and the other by a brown unicellular alga, and of how they have given up eating solid food after the manner of animals, because they are entirely dependent on their lodgers is interesting enough and partly familiar already. But the further story of how each species of worm exhibits a series of extremely regular and astonishing movements, in relation to the tides, which result in constantly keeping it in the ideally best position in which to carry on its life, of how these movements can be analysed, by suitable experiments in the laboratory, into a series of "tropisms," impressed rhythms, and "tones," of exactly the same nature as those with which the plant-physiologist is familiar in the reactions to light and gravity of the higher plants, the whole combining to adapt the "plant-animal" perfectly to its sharply defined place in nature, constitutes a study of quite exceptional charm.

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[1] "Plant-Animals: a study in symbiosis," by Frederick Keeble. Pp. viii and 163. Cambridge, at the University Press, 1910. Price One Shilling.

Not less attractive is the record of how Professor Keeble solved the problem of what the alga which forms the green cells of *Convoluta roscoffensis* really is, and how it gets into the animal; of the anxiety of the animal to receive its guest, of its wretched condition when "infection" is prevented, and of how when the alga is safely ingested, both host and lodger live a life of enervating luxury, the alga on the nitrogenous waste products of the worm, the worm on the carbohydrates of the alga; of how, probably owing to the gradual waste of nitrogen, an end comes to this delightful arrangement, the animal is forced to digest its benefactor, which has lost its cell-nucleus and is unable to resist the process. Both organisms have found a short cut to a livelihood, the animal gives up its power of eating solid food and finally dies as the result, but since it is still able to reproduce its species, it has, biologically, the best of the bargain. The plant, driven by the nitrogen famine of the open sea, finds abundance of food and a perfectly protected home, for a time (!) in the body of the animal. Those individuals which choose this easy path lose their power of reproducing their kind—the species is maintained by the self-dependent autophytic individuals which remain outside.

HEREDITY.

MR. Doncaster's little book[1] in the same series is a very able and clearly written summary of the present position of our knowledge of heredity, characterised by a judicial readiness to give full weight to rival schools, which is unfortunately rather rare with writers on this subject. It may be cordially recommended as an introduction to the subject, and to those who lack time or inclination for further study A.G.T.

The Cambridge Manuals of Science and Literature, edited by P. Giles and A. C. Seward, is the general title of a new series to which both these books belong, issued by the Cambridge University Press. They are intended to be "short books in which recent discoveries or modern tendencies are treated with semi-popular and broad style" .... "not in any sense general text-books but essays on particular branches of knowledge." The series, which has certainly made a good beginning, promises to contain many interesting and attractive volumes, and the very low price of each (one shilling) will place them within easy reach of a wide circle of readers. The general title is, perhaps, not very happy; a "manual" rather conveys the idea of the detailed hand-book, the "stodgy" if necessary occupant of the laboratory or study table.

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[1] "Heredity in the Light of Recent Reseach," by L. Doncaster. Pp. x and 140. Cambridge, at the University Press, 1910. Price One Shilling.

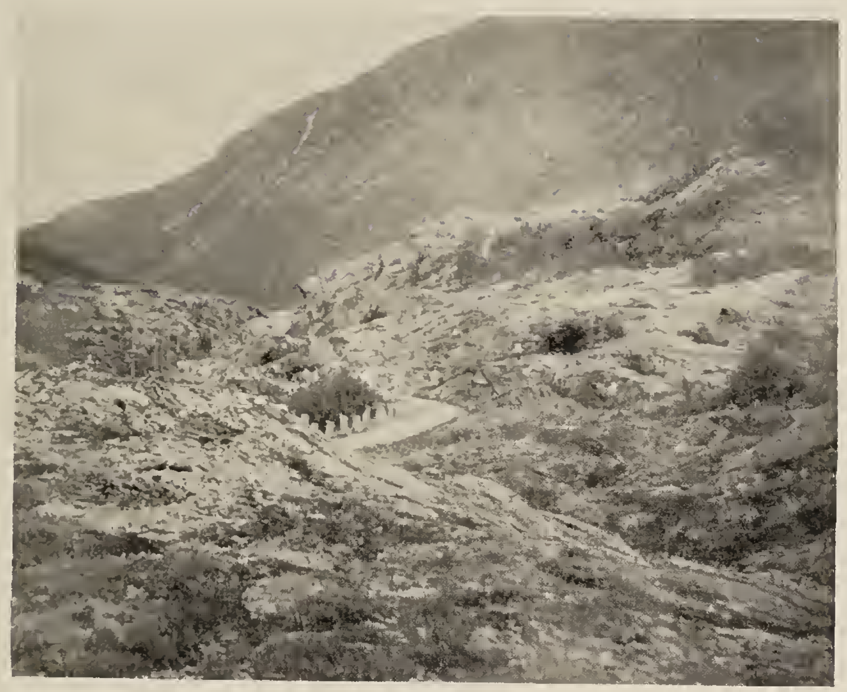

Fig. 1.

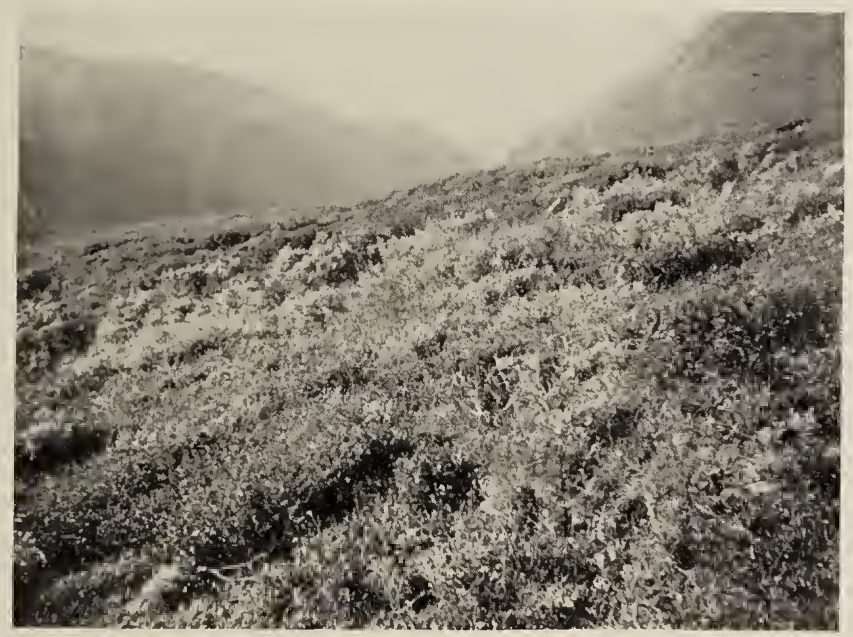

Fig. 2.

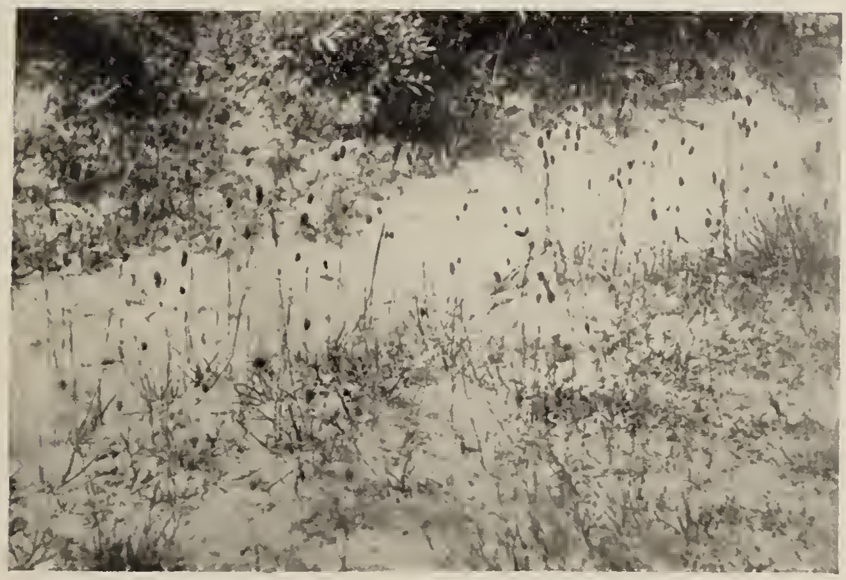

Fig. 3.

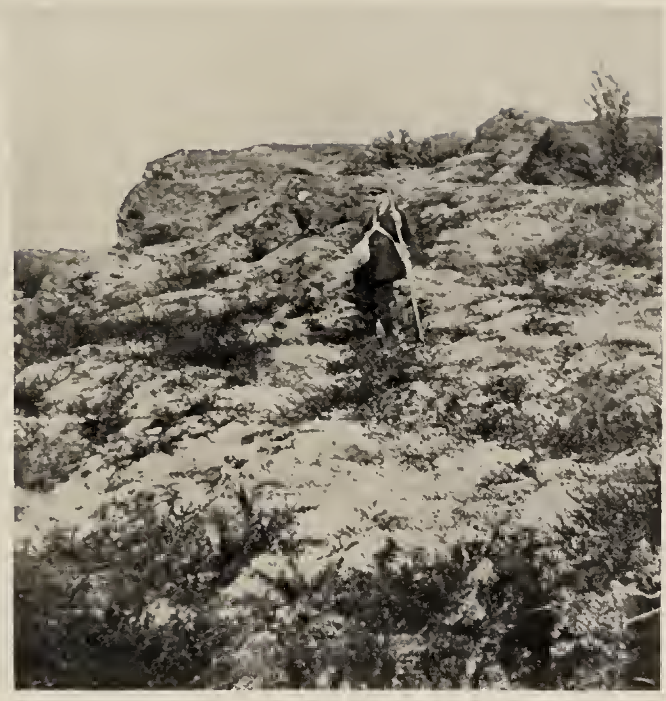

FIG. 1.

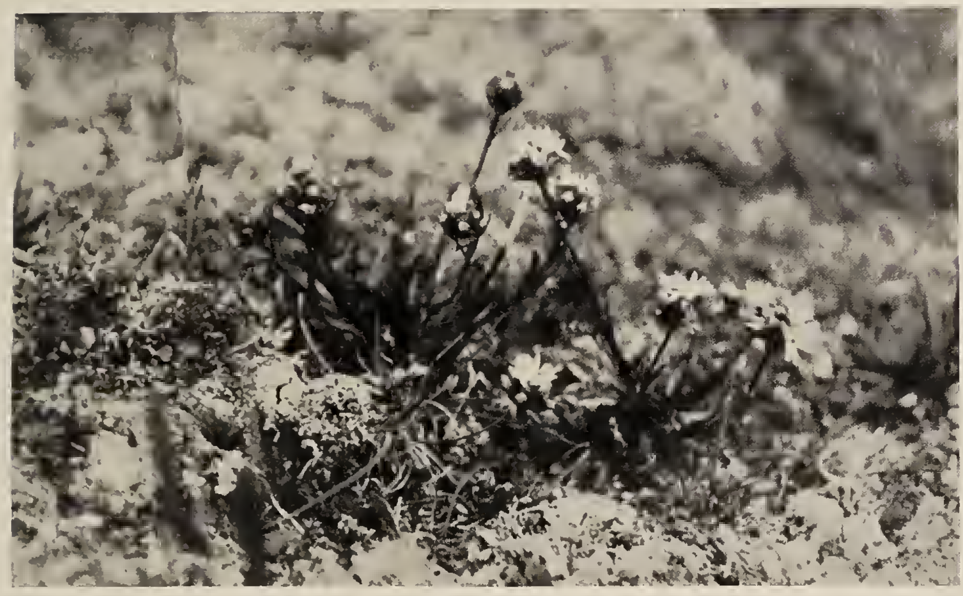

FIG. 2.

FIG. 3.

W. & G. S. WEST — ECOLOGY OF DRIVA VALLEY.

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THE INTER-RELATIONSHIPS OF THE BRYOPHYTA,

By F. Cavers, D.Sc.

V. ANTHOCEROTALES.

IN Schiffner's account of this family in Engler and Prantl (32), three genera are distinguished: *Anthoceros* (cosmopolitan, with 79 species), *Dendroceros* (tropical, with 15 species), and *Notothylas* (temperate and tropical, with 9 species.) At the present time, the number of species described stands at about 120, all growing on damp soil with the exception of a few *Anthoceros* species, which occur on decaying wood, and of all the *Dendroceros* species, which are epiphytic on the stems and even on the living leaves of tropical trees.

In most species of *Anthoceros* the thallus is, as in the widely distributed *A. lœvis*, several cells thick at the middle and thins out to a single layer at the margin, where there are numerous growing points each occupying a notch. The apical growth can usually be referred to a single initial cell, from which segments are cut off above, below, and on either side. The further divisions of the segments are very regular; each upper and lower segment divides first into an inner and an outer cell, the inner cells derived from both segments giving rise to the central tissue of the thallus, while the sexual organs on the upper side and the rhizoids and *Nostoc*-cavities on the lower are derived from the outer cells of the segments. The thallus branches repeatedly and rapidly, and often in such a regularly dichotomous manner as to form a more or less regular disc, or rosette, of circular outline. When branching is about to occur, the apical cell divides so as to form a row of cells lying side by side, and the middle cells then grow out and form a projection ("middle lobe") separating the two new growing-points.

These middle lobes usually remain small, but in some species they grow into conspicuous appendages, often toothed, which serve to retain water by capillarity and also to increase the assimilating surface of the plant. The same purpose is served by the leaf-like outgrowths on the upper side of the thallus in some species; in *A. fusiformis* these are lamellæ of varying sizes and shapes, while in *A. arachnoides* the whole plant is covered with hair-like or plate-like outgrowths forming an irregular network of shallow water-holding chambers. In *A. giganteus* the thallus is sharply divided into a massive midrib and one-layered wings, the lobes of the latter being folded over towards the underside and forming hood-like water-cavities.

Many species of *Anthoceros*, especially those which grow in dry situations, have perennating tubers in which food is stored and which persist after the rest of the plant has died down. In most cases these tubers arise on the edge of the thallus, probably always from a growing-point, and either remain as swollen bodies slightly buried in the soil, or they may become stalked and pushed well below the surface. Examples of tuber-bearing species have been figured by Howe (14) and by Goebel (9); as was shown by Ashworth (1), the tuber has a firm envelope of corky cells, while the inner cells contain proteid-grains and oil-drops.

The tissues of the thallus are usually almost uniform, though the central cells are often, especially in the older parts of the thallus, greatly elongated and have their walls reticulately thickened. Though not forming a very definite strand, these cells may perhaps be compared with the pitted cells forming the conducting tissue in such Liverworts as *Pallavicinia*, but it must be remembered that similarly thickened cells often occur in the Marchantiales. In several species of *Anthoceros* there occur cavities of irregular shape and size, which are formed by splitting apart of the cells and contain abundant mucilage. In *A. dichotomus*, of which the writer has examined abundant fresh material, these mucilage sacs are sometimes inhabited by *Nostoc*, the chains of this alga having apparently entered the otherwise quite closed sacs by way of the intercellular spaces; in some cases the *Nostoc* chains were seen to be connected with the normal *Nostoc*-cavities which at first open by a stoma-like slit on the underside of the thallus. The *Anthoceros* thallus does not bear the special gum-forming hairs which are so common in Liverworts, but the special mucilage-slits, to be described presently, keep the growing-point bathed in gummy liquid. Indeed all the tissues contain abundant mucilage, which escapes when the thallus is cut into.

The thallus shows two vegetative features of special interest, the peculiar chloroplasts and the *Nostoc*-cavities. In nearly every cell there is, in most species of *Anthoceros*, a single large chloroplast, varying in form. but usually oval and flattened, with a conspicuous central pyrenoid, around which starch-grains are clustered as in various Green Algæ with similar chloroplasts. The nucleus lies in close apposition to the chloroplast, usually near the pyrenoid, and sometimes the chloroplast becomes folded so as to enclose the nucleus more or less completely. The curious *Nostoc*-cavities almost always found in the lower tissue of the thallus were described by Hofmeister (13), who mistook them for gemmæ; what he figures as cell-walls dividing up the cavity are in reality the hairs which grow in from the cells bounding the chamber after the *Nostoc* has entered by means of a slit between two of the lower superficial cells of the thallus. The real nature of these cavities was discovered by Janczewski (17) and Szymanski (34), while Leitgeb (22) carefully followed the development of the cavities and their infection by the hormogonia of *Nostoc* and showed how the *Nostoc*-chains grow vigorously in the enlarging cavity, the cells lining the latter growing into hairs which mingle with the alga. These cavities are primarily gum secreting organs, and Peirce (30) has recently shown that *Anthoceros* plants raised from spores in sterilised soil grow quite normally, and probably even better, in the absence of *Nostoc*.

Apart from Hofmeister's "gemmæ," which turned out to be the *Nostoc*-cavities just mentioned, there are some observations on record which seem to indicate that *Anthoceros* has special organs for asexual propogation. Hofmeister's account of small gemmæ which arise by rejuvenescence of the mother-cell and escape through a pore in the wall does not appear to have been confirmed, though gemmæ, or more correctly *gonidia*, of this nature occur in *Aneura* and *Metzgeria*. Ruge (31) has described and figured the development in *Anthoceros glandulosus* of stalked brood bodies which have a mucilage cavity and pore already formed before being detached from the parent plant.

The sexual organs of the Anthocerotales differ very markedly in certain respects from those of other Bryophytes, though their peculiarities have been somewhat exaggerated by some writers. In the case of the antheridia, either one, or (in *Notothylas* and most species of *Anthoceros*) a group, of these organs occurs in a closed cavity in the upper tissue of the thallus, roofed over by a double layer of cells, this roofing tissue being later ruptured so that the antheridia are left in a cup-like depression. According to most recent writers, the antheridium, or group of antheridia, arises from a single superficial cell which divides first by a transverse wall into an inner and outer cell, the latter dividing again by a tangential wall to form the beginning of the roof, while the inner cell divides longitudinally into four parallel cells, which either remain coherent and develop into a single antheridium, or else separate and form four antheridia. Apart from their endogenous origin, the antheridia agree in structure with those of the Sphærocarpales. The number of antheridia in each cavity varies a good deal in different species of *Anthoceros*, and in different individuals; there may be as many as nine or ten. As first described by Leitgeb (23), exogenous antheridia sometimes occur in *Anthoceros*, evidently through an inversion of the normal course of development—*i.e.*, the upper half of the primary cell gives rise to the body of the antheridium and the lower to the stalk. Frau Lampa (18) has described, as exogenous antheridia what appear to be in reality the early stages of the tubers found in *Anthoceros dichotomus*. Though the occurrence of exogenous antheridia is apparently a rare abnormality in *Anthoceros*, it probably represents a reversion to a primitive condition, and it would be interesting to ascertain whether it occurs in other species of *Anthoceros* besides *A. lævis*, and in the remaining genera of the group.

The archegonia of the Anthocerotales are not only sunk in, but are from the beginning histologically continuous with, the tissues of the gametophyte. However, the cell-divisions that occur in the developing archegonium are exactly the same as in the other Liverworts; the mother-cell does not project from the surface, but it undergoes the usual three primary intersecting divisions, cutting off the peripheral cells (which in other Bryophytes form the venter and neck) from the central cell which divides to form the usual axial series of the Liverwort archegonium (cover-cell, neck-canal-cells, ventral-canal-cell, oosphere). The cover-cell-group often projects slightly, and it would be of great interest if cases were discovered in which more or less of the neck is free. As it is, the difference between the Anthocerotean archegonium and that of other Bryophytes is merely one of degree, and the gap is to some extent bridged over by *Aneura*, where the venter is embedded in and continuous with the thallus tissue, instead of being entirely free on the surface.

The oospore divides by longitudinal and transverse walls so as to form three tiers of four cells each, and in all probability these tiers give rise to the three regions of the mature sporophyte—the more or less bulbous foot, the meristem, and the capsule. The cells of the upper tier are next divided by walls which cut off four central cells from a layer of outer cells; but now the course of development diverges from that typical of other Liverworts. In the latter, the central tissue (endothecium) becomes the sporogenous tissue, but here it remains sterile and forms an actual rod or columella, while the archesporium is cut out of the peripheral layer and, moreover, is hemispherical, extending over the apex of the columella (this is the case with the *fertile* portion of the archesporium in *Pellia*). The original four rows of cells forming the columella increase to sixteen rows, the archesporium becomes two-layered, and the capsule-wall becomes about four cells deep, the outermost layer forming a sharply marked epidermis with cuticle and stomata. The cell-divisions in the meristem zone below the capsule correspond with those in the capsule region of the embryo, and owing to the active growth of this zone the capsule continues to elongate for a considerable time, additions being made to columella, archesporium, and wall. The archesporial cells become differentiated into large globular spore-mother-cells and variously shaped sterile cells which remain irregularly united to form a network. The cells forming the sporogonial wall are separated by air-spaces which communicate with the stomata in the epidermis, and each cell contains *two* chloroplasts. The stomata are quite like those of the Vascular Plants; each is formed by splitting of a cell which has remained oval while the surrounding epidermal cells have become elongated. As the spores ripen, the capsule-wall splits, from the apex downwards, into two valves, between which the thread-like columella projects. The columella has a mechanical function in strengthening the long sporogonium and holding together the network of sterile cells with the spores in its irregular meshes, but its primary function is doubtless that of transporting water and salts, absorbed from the thallus by the foot, to the green assimilating tissue of the capsule-wall, by way of the sterile cells, as well as to the developing sporogenous tissue. The sterile cells when young contain abundant starch and proteids. The developing spores are therefore very efficiently supplied with food by means of the columella, the sterile cells, and the green tissue, and their rapid development is obviously due, as pointed out by Goebel (10) to these favourable arrangements for their nutrition. The sterile cells of *A. lævis* are thickened along two opposite sides of the wall, which in some cases even shows distinct spiral thickening bands. The latter are well developed in *Dendroceros* and in certain species formerly included in *Anthoceros*, but now transferred to Campbell's new genus, *Megaceros*. There can be little doubt, from actual observation, that even in *A. lævis* the sterile cells perform, as their final function, some service in aiding spore-dispersal by means of hygroscopic movements. For some time the surrounding tissue of the thallus, into which the bulbous foot penetrates deeply and sends haustorial outgrowths of its outer cells, keeps pace with the growth of the sporogonium and grows up as a sheath, which is eventually broken through at the tip. The capsule reaches a length of as much as four inches in some species, giving fruiting patches of the plant the appearance of fine grass, and continues to grow for months. In germination, the spore-contents usually give rise to a longer or shorter germ-tube, at the end of which a cell-mass is formed, but sometimes the tube is suppressed; in any case the cell-mass soon shows an apical cell, rhizoids, mucilage slits, and apical branching.

In *Dendroceros*, the plant-body is distinguished into a thick and usually broad midrib with one-layered lateral wings, which are folded and often regularly lobed, showing an approach to the *Fossombronia* type with distinct leaves. Some species are definitely foliose, and in *D. foliatus*, discovered by Spruce (33), large hood-like structures are developed from the "middle lobes" formed in branching, in addition to smaller hidden appendages which represent the ordinary lobes or leaves. As in *Anthoceros* there are *Nostoc*-cavities, and in some species large intercellular cavities in the midrib, giving the latter an areolated appearance like that of a Marchantiaceous thallus. The development of this genus has been chiefly worked out by Leitgeb and by Campbell (3). The apical cell is semi-circular, segments being cut from it in a single series. The antheridia are solitary, large, and long-stalked the stalk is coiled up within the cavity, the roof of the latter projecting strongly above the surface of the thallus. The sporogonium on the whole resembles that of *Anthoceros*, except that the archesporium extends downwards nearer to the foot and often remains in parts only one cell thick, the sterile cells becoming joined end to end and forming definite elaters with a well-marked spiral band ; there are no stomata on the capsule. In some species the spores begin to germinate before being set free, forming multicellular bodies, as in *Pellia* and *Fegatella*.

Notothylas shows a close general resemblance to *Anthoceros* in its gametophyte and sexual organs, but the sporogonium presents some interesting points of difference and has given rise to much discussion and conflicting opinion. Lang's recent work on this genus (20) has added considerably to our knowledge of the sporogonium and its development. The earlier observers Milde (26, 27, 28) and Gottsche (12) held that the columella of *Notothylas* might either be present or absent in different plants of the same species, and that it might be either intact and well-developed in mature or nearly mature capsules, or might be broken into fragments, or represented by a short projection at the base of the capsule. Leitgeb confirmed these observations, but showed that when the columella was absent this was not due to breaking up into its constituent elater-like cells, as Gottsche had suggested. Leitgeb further concluded that while the first divisions of the embryo were like those of *Anthoceros*, the central (endothecial) cells cut off by the first periclinal walls gave rise to the archesporium and that the columella was subsequently differentiated within this central tissue or endothecium. Leitgeb found the columella well developed in some specimens of *N. Breutelii*, while in others there was hardly a trace of it even at the base of the capsule, and on the view that the whole sporogenous mass is derived from the endothecium and the columella arises by later differentiation within it, he suggested that this genus forms a link between the other Anthocerotales on one hand and the Jungermanniales on the other, comparing the columella of *Notothylas* to the axile bundle of sterile elater-like cells which springs from the base of the capsule of *Pellia*.

According to Mottier (29) and Campbell (2) the development of the sporogonium in *Notothylas orbicularis* is much the same as in the other Anthocerotales, except that the archesporium becomes very massive in its upper part where it extends over the apex of the columella. These writers confirm Leitgeb's account, however, as to the regular alternation of alternate zones of sterile and fertile tissue in the archesporium, and the occurrence of curved thickenings on the sterile cells and also on the cells composing the columella. Lang's account is much more complete and conclusive, and he sums up the chief features of the sporogonium in the species he investigated (*N. Breutelii*) by saying that "the embryogeny conforms to the usual type for the Anthocerotaceæ, but that the endothecium, instead of being devoted to the formation of a sterile columella, forms sporogenous tissue for the greater part of the intercalary growth of the sporogonium. In a considerable proportion of cases, however, it produces sterile tissue towards the close of development." His observations show that the endothecium must be regarded as potentially sporogenous, a fact which, according to this writer, "increases the justification for considering the central group of cells, which in all other Anthocerotaceæ is wholly devoted to the formation of a sterile columella, as the original sporogenous tissue and the amphithecial archesporium is of secondary origin. The duty of producing spores would seem to have been transferred from the central to a more superficial set of cells." Lang inclines to the view that the species of *Notothylas* are reduced forms, since "the appearance of the archesporial layer derived from the amphithecium, even when the central cells are fertile, suggests an origin from forms with a sterile columella."

Among some specimens from the herbarium of Mr. W. H. Pearson, the writer found a species of *Anthoceros* (*A. Hallii*, Aust.) which differs considerably from the rest of this genus and approaches closely to *Notothylas*. The sporogonium of *Notothylas* is very small and when ripe projects but slightly beyond the "calyptra" or sheath; its epidermis has no stomata; there is practically no assimilating tissue; and the inner layers of the capsule-wall soon become disorganised (probably serving to nourish the developing spores). In *Anthoceros Hallii* the capsule (4 to 7 mm. long) projects beyond the sheath for less than one-third of its length. The projecting apical portion bears a small number of remarkably large guard-cells; each cell of the capsule-wall contains two large chloroplasts; the columella does not extend into the projecting tip of the sporogonium; and the sterile cells have the stumpy flattened form characteristic of *Notothylas*, and bear irregular fibrous thickenings. *Anthoceros Hallii* appears to form an almost perfect connecting-link, in such characters as can be made out from herbarium material, between the small-capsuled species of *Anthoceros* on one hand and the forms included under the genus name *Notothylas* on the other.

It has long been known that certain species hitherto included in the genus *Anthoceros* resemble *Dendroceros* in having the sterile cells developed as elaters with spiral bands, and in the absence of stomata from the capsule-wall. Campbell (4, 5, 6, 7) has recently investigated a number of these species and has proposed the formation of a new genus, *Megaceros*, for their reception, the name being suggested by the large size of the sporogonium in most of these forms. This genus is further distinguished from *Anthoceros* by having green spores, a solitary antheridium, and as a rule several chloroplasts in the thallus-cells instead of a single large chloroplast. This new genus presents interesting points of contact with the other three genera of Anthocerotales. It resembles *Anthoceros* in the form of the thallus and its apical growth, and in the form and size of the sporogonium; *Notothylas* in the large amount of sporogenous tissue developed in the apical region of the sporogonium, above the columella; and *Dendroceros* in the characters already mentioned above, also in the green spores and the early development of the embryo.

The facts at present known concerning the morphology of the Anthocerotales appear to the writer to suggest that (i.) the forms constituting Campbell's genus *Megaceros* are at least as sharply separated from the other species of the old genus *Anthoceros* as are those comprised in the genus *Notothylas*; (ii.) the species of *Dendroceros* form a still more natural group; (iii.) it is an open question whether *Notothylas* is a reduced form. The organisation of the *Notothylas* sporogonium need not necessarily be interpreted as due to reduction from the *Anthoceros* type; the reverse interpretation does not appear to be excluded by the fact that both the endothecial and the inner amphithecial tissues produce spores. Apart from the close agreement of its gametophyte with that of *Anthoceros*, we find in the *Notothylas* sporophyte a series of forms showing varying and unfixed sterilisation of the central tissue, with progressive shifting of spore-production to the inner layer of the wall-tissue. Assuming the absence of reduction in the *Notothylas* types, we might regard *Anthoceros Hallii* as forming a link between the more primitive forms of *Notothylas* and the species of *Anthoceros* with stomata and well-developed assimilating tissue, while *Megaceros* and *Dendroceros* have arisen independently from the primitive forms of *Notothylas*, in which the sterile cells of the archesporium are short and isolated, the assimilating tissue of the sporogonium is feebly developed, and stomata are not formed. If we regard the typical *Anthoceros* capsule, with its stomata and its efficient assimilating arrangements, as being primitive, we must assume that all the other Anthocerotales have been derived from this type by more or less extensive reduction.

Various writers have emphasized the characters which mark off the Anthocerotales from the remaining Hepaticæ, and in 1897 Gayet (8) proposed to raise the Anthocerotales to the rank of a class co-ordinate with the Hepaticæ, restricting the latter term to the Marchantiales and Jungermanniales. The class was named Anthocerotes by Howe (14), who defined it in the formal systematic way, enumerating the peculiarities of the class as follows: "(i.) a single large chloroplast to each cell, instead of several smaller chloroplasts as in the assimilative tissues of the Hepaticæ proper; (ii.) the antheridia arise within the thallus—are endogenous in origin—and the walls of the immersed archegonia are confluent with the adjacent tissues; (iii.) the presence of meristematic tissue in the capsule near its base, by the activity of which the capsule has a long continued growth, ripening spores towards its apex while forming new spore-mother-cells below; (iv.) the presence, in probably all cases, of a columella around which the archesporium is formed; (v.) the presence, in many cases, of stomata on the capsule, with accompanying assimilative tissue. These five characters are peculiar to the Anthocerotes as distinguished from the Hepaticæ proper, and they are characters of much significance. For analogies we must look chiefly in two directions—toward the Pteridophyta and toward the Musci."

In the writer's opinion, the significance of these characters of the Anthocerotales has been much exaggerated, and upon them has been based a certain amount of very doubtful speculation regarding the relationships of the Archegoniatæ and the origin of the Pteridophyta. From the summary presented here, it will be seen that very little importance can be attached to the first and second of the characters mentioned above. The number of chloroplasts per cell varies considerably. The "endogenous" origin of the antheridia is obviously a secondary character, derived from the normal exogenous type of antheridium development; the antheridia themselves agree closely with those of other Hepaticæ, especially Sphærocarpales, and though the development of the antheridial cavity is peculiar, it is easier to relate it to what is found in other Hepaticæ than to establish analogies with the Pteridophyta. In the immersion of the archegonium in the thallus, the Anthocerotales do not in reality differ widely from other Hepaticæ; the archegonium is partly embedded in *Aneura*, though in this case the neck is free. The meristematic tissue above the haustorium of the sporogonium in Anthocerotales evidently results from the persistence of a stage which is quickly passed through in the development of the sporogonium in other Hepaticæ. In *Pellia*, for instance, the cells of the seta are arranged in regular longitudinal rows, owing to repeated transverse divisions in the cells between haustorium and capsule, and we may imagine the sporogonium of Anthocerotales to have arisen through the persistence of the meristematic activity of this zone of tissue, the differentiation of the capsule being deferred and becoming basipetal, instead of taking place early and being simultaneous. The columella of the Anthocerotean capsule, again, may be compared with the incomplete sterilisation of central tissue which results in the formation of the elaterophore of such forms as *Pellia*, *Aneura*, and *Gottschea splachnophylla*. It is doubtful whether much stress should be laid on the presence of stomata in the epidermis of the *Anthoceros* capsule; this feature is doubtless to be correlated with the development of a many-layered capsule-wall consisting of assimilative parenchyma. In various Jungermanniales, the capsule-wall is many-layered, and when young contains chloroplasts—a condition which persists in the Anthocerotales, but is also found in the ripe capsules of forms like *Riella*, where the cells of the capsule-wall do not become thickened with fibres in connection with a special dehiscence mechanism.

It seems probable that the Anthocerotales have arisen from forms like the Sphærocarpales, along a well-marked line of development which has led no further, and which is marked mainly by the "endogenous" origin of the antheridia and by the retention of a basal meristematic zone in the sporogonium. The antheridia were doubtless originally exogenous, and instead of becoming surrounded by an envelope (as in Sphærocarpales) or sunk in an open pit (as in Marchantiales and various Anacrogynous Jungermanniales), they have become sunk in a closed cavity formed by splitting of the walls between the antheridium-forming hypodermal cell and the surrounding thallus cells. The occurrence of a group of antheridia formed by longitudinal splitting of the young antheridium, is clearly a secondary character, just as is the process of budding which leads to the formation of more than four antheridia in a cavity in some species of *Anthoceros*. All the distinguishing characters of the Anthocerotean sporogonium are more or less definitely correlated with the persistence of the basal meristematic tissue, and are connected with the nutrition of the spores. The basal meristem produces sporogenous tissue which becomes carried up and thus separated more and more widely from the tissues of the gametophyte. In this way there is set up a demand for more elaborate and more permanent nutritive arrangements than are required in the other Hepaticæ, in which the developing sporogonium is until maturity more or less completely surrounded by the tissues of the gametophyte.

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SKETCHES OF VEGETATION AT HOME AND ABROAD.

V.—The Ecology of the Upper Driva Valley in the Dovrefjeld.

By W. West, F.L.S., and G. S. West, M.A., D.Sc., F.L.S.

[Plates III and IV and Text-Figs. 26—32].

In 1909 we spent the month of August in the upper part of the Driva Valley, making our head quarters at the Kongsvold posting-station, which lies towards the northern limit of the Dovrefjeld. Every day, in sunshine, rain, or snow, we were investigating the valley or the surrounding mountains, with the result that we accumulated much botanical material and information.

The district was reached *via* Christiania and Lille-Elvedal, leaving the train at the last-named place (alt. 1660 feet) and driving for the next 61 miles along the only road which traverses this part of Norway. The difficulties of the road, combined with the temperament of the Norwegian horses, gave us ample opportunity to gain some knowledge of the flora of the interesting botanical country through which we passed. A few preliminary notes on this flora will probably be of interest.

Among the first plants noticed on leaving Lille-Elvedal were *Carum Carui* in the more open places, *Aconitum septentrionale* in the shade, and the three colour-forms of *Saxifraga aizoides* on the wet banks. In Britain we have only the yellow form, but the orange and deep brownish-red forms here make lovely patches of colour. In the woods bordering the road were *Moneses uniflora*, *Pyrola rotundifolia*, *P. media*, *P. secunda*, and large masses of *Linnea borealis* in full flower. The first straggling specimens of *Betula nana* were also observed. On the rocky banks of the River Folla were *Carex bicolor* and *Primula stricta*, while on a neighbouring wet slope were *Carex ustulata*, *Tofieldia palustris*, and other hill-plants of wet places. On drier and more stony ground *Arctostaphylos Uva–ursi* and *A. alpina* were plentiful, and the grasses *Festuca rubra* and *Poa alpina* became dominant constituents of the road-side flora.

A fine bank of that beautiful grass *Triticum violaceum* was passed, and shortly afterwards in the shade of some dense bushes by the river-side we found a number specimens of *Pedicularis Sceptrum-Carolinum*. This *Pedicularis*, with its large yellow flowers surmounting stout stems about 18-inches high, and with a perpendicularity almost mathematical in its exactness, was certainly one of the most striking plants we observed in Norway. On the banks of detritus in the river-bed, and without doubt brought down from higher altitudes, were many alpine plants, among them being *Cerastium alpinum* and *Gentiana nivalis* associated with *Calamagrostis stricta*. One of the most conspicuous plants on the sandy banks of the Folla was *Myricaria germanica*, and the purpose of the comose appendages to the seeds was finely demonstrated in the wind.

After driving 42 miles we were most hospitally entertained at Dalholen, an ancient habitation surrounded by and built upon glacial sand. *Androsace septentrionale* was observed both in the dry sandy places and on the turf-roofs of the one-storeyed wooden buildings. In the sand were quantities of *Botrychium Lunaria* showing considerable variability both in the sterile leaf and in the fertile portion. In the immediate vicinity of several tiny brooks was an abundance of *Epilobium alsinifolium*, while near the river, in places which must be inundated on the melting of the snows, were *Polygala amara*, *Carex bicolor* and *C. capillaris*.

Between Dalholen and the river, *Platysma juniperinum* occurred *on the sand*, a most peculiar habitat, as it usually occurs on the old branches of *Juniperus nanus*, a situation in which we afterwards found it in quantity and with fine apothecia.

Towards Hjerkin the roadside was carpeted with fine fruiting specimens of *Salix herbacea*, and *Anemone vernalis* with its feathery fruits was another conspicuous roadside plant. In a bog just beyond Hjerkin, in which *Eriophorum vaginatum* was the dominant flowering plant, the moss *Paludella squarrosa* was very abundant, often associated with *Hypnum trichoides*, and by the the margins of a small stream *Thalictrum alpinum* and *Pedicularis Lapponica* were both observed in a fruiting state.

In some boggy pools close to the roadside was a tiny form of *Utricularia minor*, considerably smaller and more delicate than any that we have previously observed. It was merely a diminutive form, as its structure was quite normal.[1] The maximum diameter across the leaves was between 4 and 5 mm.

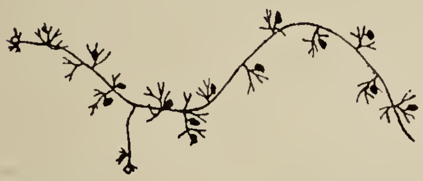

Fig. 26. Very small form of *Utricularia minor* from Hjerkin. Natural size.

About Hjerkin the region of pines was left behind, and there is a striking absence of them from the upper portion of the Driva Valley. All around the head of this valley, and on the surrounding mountains, one feature impresses itself on the mind beyond all others, namely, *the abundance of Lichens*. Fruticose and crustaceous lichens occur in prodigious quantities, covering all rocks, and often carpeting square miles of the surface of the ground.

Down the valley, from its commencement at the northern limit of the dreary elevated expanse between Hjerkin and Kongsvold, the zones of montane woodland, alpine shrubland, and alpine grassland are very clearly marked. To the south of the Kongsvold, and on the right side of the Driva, is an extensive rocky area, and similar areas of rock occur at the bottom of the

[1] Precisely the same minute form of *Utricularia minor* was obtained in a bog at the margin of Goveli Vand, the small lake S.S.E. of the Kongsvold. The bladders contained numerous individuals of *Cosmarium prægrande*, Lundell, an arctic type of Desmid only very rarely observed from Scandinavia, Finland and Greenland, of which the detailed characters have not yet been fully investigated. This Desmid was recorded in 1894 from Glen Shee, Perthshire.

valley several miles to the northward. In the immediate vicinity of the Kongsvold station are several rocky and hilly pastures, and also two small, but very productive, meadows.

In giving a brief outline of the plant-associations of this district of the Dovrefjeld we will begin with the semi-cultivated land close to the Kongsvold, and then deal successively with the woodland, shrubland, and other areas. The flowering plants and the dominant cryptogams are included in this account, but the Algæ, of which we made extensive collections, are reserved for special treatment.

1.—MEADOWS AND PASTURES.

[Marked P on the Chart on page 357].

These were undulating stony fields, about six in number, which had been reclaimed from the lower slopes near the river. The total area was small, and the best use of available space had been obtained by the removal of quantities of rocks and stones.

The common grasses were *Festuca rubra*, *F. ovina*, *Phleum alpinum*, *Avena pubescens*, *Anthoxanthum odoratum*, and *Aira cæspitosa*, the first-mentioned being the dominant one. Among the grasses five plants stood out conspicuously, viz:—*Alchemilla vulgaris*, *Ranunculus acris*, *Lychnis dioica* (with extra-large flowers), *Polygonum viviparum*, and *Stellaria media*, the latter sometimes forming a dense undergrowth to the exclusion of most other plants. *Rhinanthus Crista-galli* and several forms of *Euphrasia* were also abundant. Scattered among the plants just mentioned were individuals of the following species:—*Achillea Millefolium*, *Leontodon autumnale*, *Matricaria inodora*, *Parnassia palustris*, *Carum Carui*, *Rumex Acetosa*, *Plantago media*, *Stellaria graminea*, *Cerastium triviale*, *C. alpinum*, *Campanula rotundifolia* (with very large corollas), *Trifolium repens*, *T. pratense*, *Vicia Cracca*, *Gentiana campestris*, *Scabiosa arvensis*, and wherever there was partial shade and shelter, *Aconitum septentrionale*.

In stony places near the river were *Gentiana campestris*, *G. tenella*, *G. nivalis*, *Antennaria dioica*, and a form of *Carex Goodenoughii*.

Where the rocks abutted were *Potentilla Crantzii* (in some places this was very abundant), *Rumex Acetosella*, *Cerastium alpinum*, *Woodsia alpina*, and *Cystopteris fragilis*. The chief Bryophytes were *Hypnum rugosum*, *Polytrichum piliferum*, *Dicranum fuscescens*, and *Ptilidium ciliare*. The lichens were chiefly *Placodium elegans*, *Cladonia cervicornis*, *Cl. coccifera*, and varieties of *Parmelia saxatilis* and *P. sulcata*.

2.—Exposed Rocks near the Road.

[Marked R in the Chart].

This area of exposed rocks was many acres in extent, and occupied the lower slopes near the road and the river (Pl. 3, Fig. 1).

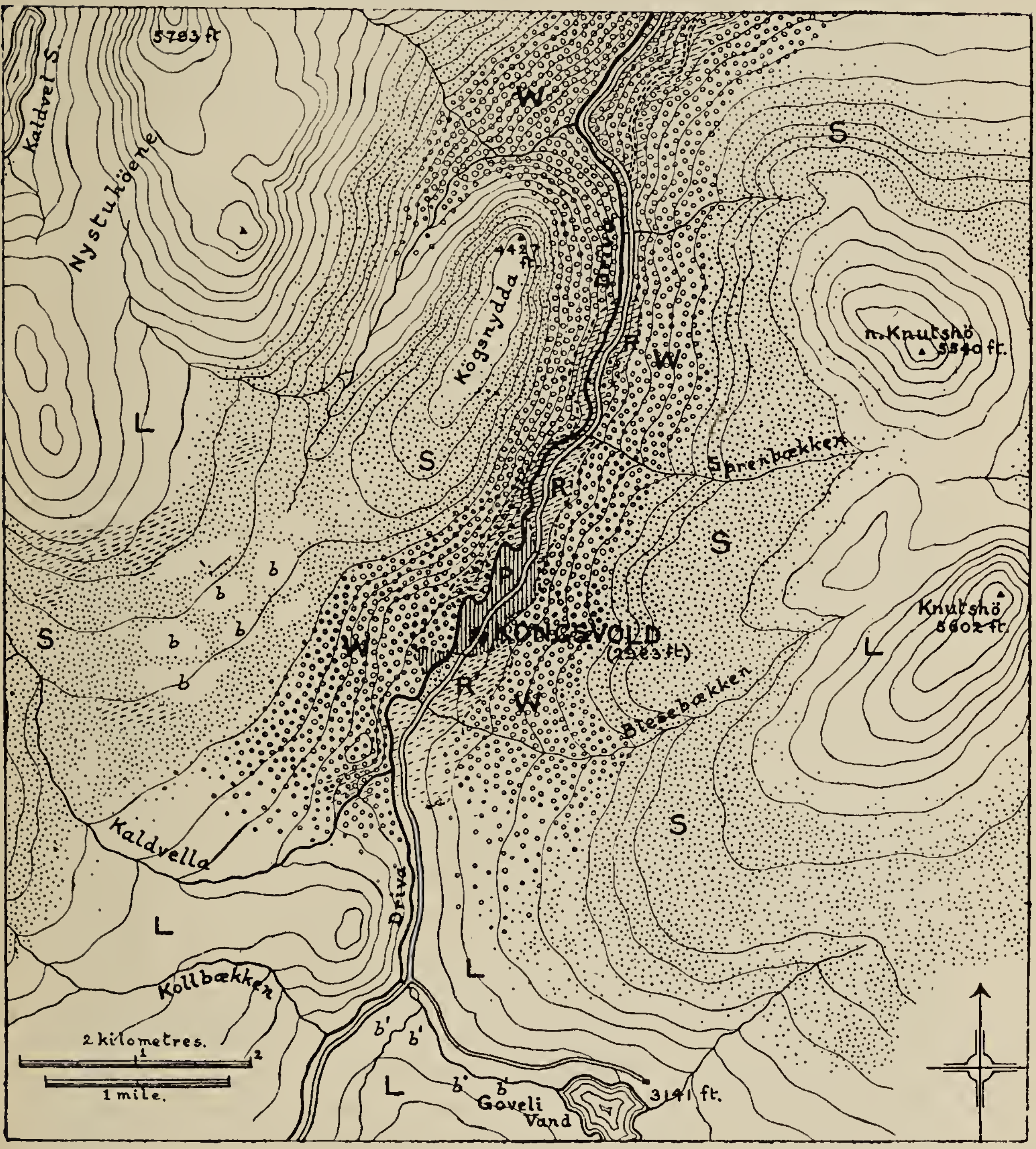

CHART OF UPPER DRIVA VALLEY.

P MEADOWS and PASTURES.

W WOODLAND. [Betula odorata f. alpigena]

S SHRUBLAND. Salix spp., Betula nana, Juniperus nanus.

R EXPOSED ROCKS. Down the valley: somewhat sheltered.

R' EXPOSED ROCKS. At head of valley; rather bleak.

L LICHEN FORMATIONS.

b and b', spongy bogs

The position was to some extent sheltered, and the flora was very characteristic. Flowering plants existed only in the hollows and cracks, and the dominant plant was *Empetrum nigrum* (40).[1] In the smaller crevices *Festuca rubra* (25) was very conspicuous, and *Arctostaphylos Uva-ursi* (8), *Poa alpina* (8), *Hieracium alpinum* (5), and *Erigeron uniflorus* (5) were in evidence in most places. Occasional specimens of *Dryas octopetala*, *Saxifraga Cotyledon*, *Alsine rubella*, and *Juncus trifidus* also occurred. *Betula nana* and *Vaccinium uliginosum* were locally distributed.

Mosses were not abundant on these rocks. The most frequent were *Swartzia montana*, *Eucalypta rhabdocarpa* and *Dicranoeveisia crispula*, with smaller patches of one or two species of *Grimmia* and *Rhacomitrium*. Very little *Rhacomitrium lanuginosum* occurred, and it appeared to be very uncommon in this cold alpine district. Its absence was a noticeable feature to those accustomed to its great abundance in the mountainous districts of Britain.

Lichens were exceedingly abundant and finely developed, and in the less sheltered places the lichen-formation occupied at least 70 per cent. of the area, the only flowering plants being *Empetrum nigrum* with a little *Arctostaphylos Uva-ursi* and *Vaccinium uliginosum*. The dominant lichen was *Alectoria ochroleuca*, although in places *Platysma nivale* successfully competed with it. Other species in moderate quantity were *Alectoria rigida*, *Cladonia rangiferina*, *Cl. sylvatica* (especially its var. *alpestris*), *Cl. cervicornis*, *Cl. furcata*, a form of *Cladonia pyxidata*, *Stereocaulon alpinum*, *S. tomentosum*, *Sphærophoron coralloides*, *Cetraria islandica*, (and its forma *crispa*), and *C. aculeata*. Associated with *Platysma nivale* and *Cetraria islandica* was *Pycnothelia papillaria*, growing over defunct *Gyrophora*. In depressions where rock-debris accumulated were quantities of *Solorina crocea*, but *Solorina saccata* only occurred in more shady situations. On the barest parts of the rocks, especially where they were subvertical, the crustaceous lichens were the most evident, and in most cases not a single square inch of rock surface was visible (*vide* Pl. 4, Fig. 3). Beautiful patches of *Lecanora ventosa*, with their richly coloured apothecia, were the most conspicuous, the rest of the patchwork consisting of *Lecidea geographica*, *Parmelia lanata*, *P. lævigata*, *P. conspersa*, forms of *P. saxatilis*, a species of *Pertusaria* (probably a form of *P. dealbata*), and other lichens, including several species of *Gyrophora*. In odd places fine fruiting specimens of *Platysma Fahlunense* occupied a considerable space, and quite a notable feature of this area was that peculiar but characteristic lichen *Thamnolia vermicularis*, occurring in a scattered manner over other lichens and mosses, sometimes in patches, but more often as solitary plants.

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[1] The numbers in parenthesis after the specific names signify percentages.

Among the exposed rocks were fairly dry patches of turf, and in some of the hollows small peaty pools were the breeding places of numerous mosquitos.

The drier parts of this turf were tenanted principally by *Empetrum nigrum* and *Betula nana*, while amongst these two plants were scattered individuals of *Vaccinium uliginosum*, *V. Vitis-idæa*, *Arctostaphylos Uva-ursi*, *A. alpina*, *Azalea procumbens*, *Phaca frigida*, *Hieraceum alpinum*, *Antennaria dioica*, young plants of *Salix lanata*, *S. phylicifolia*, *S. glauca*, various hybrid willows, *Luzula spicata*, and *Carex rigida*. Rather feebly grown plants of *Juniperus nana* also occurred, the older branches being covered with fine fruiting specimens of *Platysma juniperinum*. Near the edges of this turf, close to the rocks, were small patches of *Alsine hirta*, *A stricta*, and *A. biflora*.

In and about the wet hollows, in which there were frequently small pools, were *Eriophorum polystachyon*, *E. vaginatum*, *Carex ampullacea*, *C. ustulata*, *C. capillaris*, *Polygonum viviparum* *Rubus Chamæmorus*, and fine masses of *Saxifraga aizoides*. Small scattered patches of *Sphagnum fuscum*, *S. rubellum*, *Amblyodon dealbatus*, *Cinclidium stygium*, *Hypnum falcatum*, *H. uncinatum* v. *abbreviatum*, and a peculiar form of *H. filicinum* also occurred.

Extensive vertical faces of rock, especially near the river, were often covered with the brilliantly coloured lichen *Placodium elegans*, the deep reddish-orange colouration having a characteristic effect on the nearer landscape.

The rocks of the roadside were sometimes almost covered with *Salix reticulata* and *Saxifraga oppositifolia ;* and rock-debris, if in the shade, was largely covered by *Cystopteris montana*. Either *Silene acaulis* or *Dryas octopetala* was occasionally dominant, and plants of *Potentilla Crantzii* were sometimes very numerous.

The composition of this rock flora varied considerably as one travelled down the road, even where the conditions were uniform. A good sample, near the Sprenboekken, was as follows:—*Poa alpina* (20), *Galium boreale* (16), *Campanula rotundifolia* (16) *Potentilla Crantzii* (16), *Achillea Millefolium* (15), *Astragalus alpinus* (9), individuals of a considerable variety of plants (8). The latter consisted largely of *Polygonum viviparum*, *Alchemilla vulgaris* var. *montana*, *Thalictrum simplex*, *Erigeron alpinus*, *E. uniflorus*, *Scabiosa arvensis*, *Cerastium alpinum*, *Silene rupestris*, *Androsace septentrionale*, *Saxifraga tridactylites* var. *adscendens*, *Gentiana nivalis*, *Astragalus Oroboides*, and others. Wherever the rocks were wet, *Saxifraga aizoides* was abundant and *Oxyria digyna*, *Carex ustulata* and *Pinguicula vulgaris* were conspicuous. The latter was observed growing almost on bare rock-faces where the trickle of water was constant. Among the less common plants by the roadside were *Stellaria borealis* and *Cerastium trigynum*, and, in moist shady places, *Viola biflora*.

Lower down the valley, on the steep rocky slopes, were fine specimens of *Asplenium viride*, *Woodsia alpina*, *Saxifraga Cotyledon*, *Potentilla nivea*, and *Carex ornithopoda*. Near the roadside were *Polemonium cœruleum*, *Papaver radicatum* (= *P. nudicaule*), and *Artemisia norvegica*.

3.—COLONISATION OF NEWLY-BARED ROCK.

Many rock-surfaces had been bared during the blasting operations in the construction of the road, and a careful survey was made of the plants which had colonised this freshly exposed rock. They had occupied the crevices and hollows of the rock in the following relative abundance:—*Silene acaulis* (20), *Empetrum nigrum* (13), *Saxifraga oppositifolia* (8), *Oxyria digyna* (7), *Polygonum viviparum* (7), *Carex atrata* (7), *Luzula spicata* (7), *Salix lapponum* (5), *Alchemilla alpina* (4), *Draba hirta* (4), *Saxifraga cæspitosa* (4), *Festuca duriuscula* (4), *Sedum Rhodiola* (3), *Artemisia norvegica* (1), and *Lycopodium Selago* (1). On the rocky ledges, tufts of *Elyna Bellardii* were occasionally observed.

Of the mosses, *Hypnum rugosum* and a form of *Rhacomitrium heterostichum* were firmly established, and plenty of *Bartramia Œderi* occurred in shady places. Many lichens had also covered the rocks. *Lecidea geographica* was in the most exposed places, *Placodium elegans* was dominant on bare rocks in the shade, and on the flatter places were *Platysma nivale*, *Alectoria ochroleuca*, *Stereocaulon alpinum*, and many others.

4.—BANKS OF DEBRIS AND RUBBLE.

These were sloping masses of rock-debris, both in the form of natural screes and as artificial banks formed during the construction of the road. Numerous plants had established themselves, and so far as was observed, in the following relative abundance:—*Salix* *glauca* (20), *Salix reticulata* (8), *Parnassia palustris* (8), *Phaca frigida* (5), *Artemisia norvegica* (3), *Sedum Rhodiola* (2), *Cystopteris fragilis* (2), *Campanula rotundifolia* (2), *Juncus trifidus* (2), and numerous other widely scattered individuals of *Bartsia alpina, Silene acaulis, Juncus castaneus, Potentilla Crantzii, Polygonum viviparum, Pinguicula vulgaris, Festuca rubra, Luzula congesta, Astragalus Oroboides, Galium boreale, Antennaira dioica*, and a number of other phanerogams. The principal mosses were *Hylocomium proliferum*, large patches of *Hypnum rugosum*, and a variety of *Dicranum fuscescens*. The lichens on the barer places were *Stereocaulon tomentosum, Platysma nivale, Cladonia rangiferina, C. sylvatica* var. *alpestris, C. furcata, Gyrophora polyrhiza, G. hyperborea, Parmelia exasperata*, and *Platysma Fahlunense*. *Nephromium arcticum* and *Peltidea aphthosa* occurred in the shade, *Peltidea venosa* was in fine fruit on the moister rocks, and *Cetraria hiascens* was practically the sole occupant of the small depressions.

5.—COLONISATION OF THE OLD ROAD.

Certain parts of the old road were entirely discarded some thirty years ago when the new highway was constructed, and they afford an interesting example of colonisation by surrounding plants. In greatest quantity were *Euphrasia officinalis, Juncus arcticus*, and *Festuca rubra*, the latter giving, in places, a red coloration visible distinctly at a distance of a quarter-of-a-mile. *Poa alpina, P. glauca* and a variety of *Luzula campestris* were not uncommon, while *Pinguicula vulgaris* was abundant in places. Other scattered plants were *Lychnis alpina, Erigeron uniflorus, Parnassia palustris, Alsine rubella. Sagina nivalis, Astragalus alpinus* and *Campanula rotundifolia*.

Creeping in from the edges were *Tofieldia palustris*, the brush-form of *Equisetum arvense*, and the various alpine willows. Seedling willows were of frequent occurrence on this old road. When the road passed between rocks, *Arctostaphylos Uva-ursi* and *A. alpina* had extended well over it, while in some of the higher parts *Antennaria dioica, A. alpina, Juncus trifidus*, and *Diapensia lapponica* occurred in abundance. Small areas were entirely occupied by a small form of *Carex incurva*, and *Botrychium Lunaria* was not at all uncommon.

Some old dead rhizomes of *Juncus arcticus* were completely covered with *Stereocaulon condensatum*.

6.—WOODLAND OF THE LOWER SLOPES OF THE VALLEY.

[Marked W in the Chart.]

A belt of woodland occurred on both sides of the valley from the river to an altitude of 3600 feet on the western side and 3700 feet on the eastern side. The trees consisted almost exclusively of *Betula odorata* forma *alpigena*, and reached a maximum height of 15—20 feet. A few specimens of *Prunus Padus* occurred in sheltered places at the bottom of the woods. *Cotoneaster integerrima* was also very rare in the lower sheltered part. The woods were on rocky slopes, sometimes very steep, and here and there, where the rocks were larger, small open spaces occurred. *Parmelia olivacea* was the only corticolous lichen at all prominent on the *Betula odorata*, and it was very abundant and often covered with apothecia. It also occurred very sparingly on the adjacent rocks.

The undergrowth was often dense, but no plants were particularly conspicuous or dominant, with the exception of dense masses of *Aconitum septentrionale* in the deep shade, and quantities of *Geranium sylvaticum* in the more open spaces. The shrubs consisted of scattered plants of *Juniperus nana*, *Betula nana*, *Salix lapponum*, *S. lanata*, *S. glauca*, *S. phylicifolia*, *S. hastata*, *and S. nigricans*, while amongst the more broken rocks were quantities of *Vaccinium uliginosum*, *V. Myrtillus*, *V. Vitis-idœa* and *Empetrum nigrum*. The latter was associated with *Arctostaphylos Uva-ursi* among the rocks of the more open parts of the woods.

The following plants occurred amongst the undergrowth on both sides of the valley:—*Campanula rotundifolia*, *Galium boreale*, *Melampyrum sylvaticum*, *Lychnis dioica*, *Primula stricta*, *Saussurea alpina*, *Erigeron elongatum*, *Solidago Virgaurea* var. *cambrica*, *Phaca frigida*, *Astragalus alpinus*, *A. Oroboides*, *Rumex Acetosa*, *Trientalis europæa*, *Maianthemum bifolium*, *Phleum alpinum*, *Poa glauca*, *Poa nemoralis*, *P. alpina*, *Festuca rubra*, *Anthoxanthum odoratum*, *Avena pubescens*, *Aira cæspitosa*, *Trisetum subspicatum*, *Melica nutans*, *Luzula parviflora*, *L. spicata*, *L. campestris*, *Cystopteris fragilis*, *Equisetum arvense*, and *E. sylvaticum*. Less common were *Achillæa Millefolium*, *Bartsia alpina*, *Spiræa Ulmaria*, *Potentilla Crantzii*, *Ranunculus acris*, *Parnassia palustris*, *Epilobium palustre*, *Vicia Cracca*, and *Carduus heterophyllus*. On and about the more rocky parts of the woods were *Salix reticulata*, *Sedum Rhodiola*, *Thalictrum alpinum*, *Saxifraga aizoides*, and *S. nivalis*. *Pinguicula vulgaris* was also common on the mossy tufts of these damp rocks, generally associated with *Luzula parviflora*.

Hylocomium proliferum, *Ditrichum flexicaule* v. *longifolium*, and *Polytrichum formosum* were the most noteworthy mosses in any profusion, *Sœlania cæsia* was decidedly rare, and hepatics were quite scarce. The only frequent one was *Ptilidium ciliare*, in large patches; *Chiloscyphus polyanthus* and *Lophozia lycopodioides* occurred here and there, and a species of *Scapania* was noticed repeatedly.

The lichens were represented by *Nephromium arcticum*, *Platysma juniperinum*, *Parmelia olivacea*, *P. physodes*, *P. lævigata*, *P. vittata*, *Cetraria islandica*, *Cladonia sylvatica*, *Cl. pyxidata*, *Pannularia lepidiota*, and *Pannaria brunnea*.

Species of *Boletus*, *Lycoperdon*, and *Russula* were not uncommon, and *Taphrina Betulæ* was responsible for numerous witch's-brooms on the dominant *Betula odorata*.

One noteworthy feature of *Astragalus alpinus* should be recorded. This plant occurred in thousands on the lower slopes of the valley, and in all observed cases *fruits were only formed and ripened in the lower flowers of the inflorescence.*

The following plants were noticed only in the undergrowth of the woods on the western (left) side of the valley:—*Draba incana*, *D. hirta*, *Valeriana officinalis*, *Carex capillaris*, and on rocks near the river, *Carex ornithopoda*. On a small muddy flat near the river was an abundance of *Ranunculus pygmæus*.

The plants noticed only in the undergrowth of the eastern (right) side of the valley were more numerous, and were as follows:—*Pyrola media*, *P. rotundifolia*, *Geum rivale*, *Rubus saxatilis*, *Alchemilla vulgaris* var. *montana*, *Archangelica officinalis*, *Chærophyllum sylvestre*, *Myosotis sylvatica*, *Viola biflora*, *Juncus castaneus*, *Carex vaginata*, *Festuca ovina*, and *Cystopteris montana*. The latter occurred only in the very shady clefts of rock, where the sunshine could never penetrate. Two willows, *Salix myrsinites* and *S. arbuscula* were not uncommon, but very local.

Lower down the valley, on the eastern side and near the old road ("Vaarstien") was a boggy flat which had the appearance of a nearly-filled-up tarn. Its area was small, but it contained much *Sphagnum*, an unusual occurrence in the northern part of the Dovrefjeld, where the bogs as a rule contain little *Sphagnum*. *Andromeda Polifolia*, *Comarum palustre*, *Rubus Chamæmorus*, and *Menyanthes trifoliata* were general, and firmly embedded in the *Sphagnum* was the rare *Pinguicula villosa*. Among the birches at the edge of this bog were fine specimens of *Ranunculus aconitifolius*, and on somewhat higher rocky ground were *Luzula parviflora*, *L. arcuata*, *Carex lagopina*, *Ranunculus nivalis*, and *R. hyperboreus*. Immense quantities of *Lycopodium annotinum* occurred both under the shade of the birches and in the more open places, and *Mulgedium alpinum* was noticed in association with *Gnaphalium norvegicum* and *Ranunculus aconitifolius*.

Near the upper limit of the belt of woodland there is a marked change in the composition of the flora and in the relative abundance of the species. The *Betula odorata* becomes reduced in height (10-15 feet) and the trees are more scattered. *Vaccinium Myrtillus* and *Empetrum nigrum* become more conspicuous. *Menziesia cœrulea*, *Circæa alpina*, *Bartsia alpina*, *Galium boreale*, *Sedum Rhodiola*, *Gentiana tenella*, and *G. nivalis* are all leading constituents of this upland undergrowth. *Luzula spicata* occurs in large patches, and wherever the ground is wet, *Carex atrata*, *C. ustulata*, and *C. pulla* are abundant. *Melandryum* (*Wahlbergella*) *apetalum* is also frequent.

7.—BELT OF SHRUBLAND.

[Marked S in the Chart].

Betula odorata f. *alpigena* ceases at 3600 feet on the W. side of the valley and 3700 feet on the E. side. Above this altitude is a dense and extensive belt of shrubs (Pl. I., Fig. 2) consisting of *Betula nana* and various willows, among which *Salix lanata*, *S. glauca*, *S. lapponum*, *S. phylicifolia*, and *S. myrsinites* are the most conspicuous. *Juniperus nana* is also much in evidence in the lower parts of the belt, but does not extend to the upper reaches of the shrubland. *Salix reticulata* and *S. herbacea* occur in small quantity.

The undergrowth at 3700 feet consists mostly of *Alchemilla vulgaris* var. *montana*, *Geranium sylvaticum*, *Bartsia alpina*, *Phaca frigida*, *Pedicularis Œderi*, *Poa alpina*, *Aira cæspitosa*, *Rumex Acetosa*, *Carduus heterophyllus*, *Saussurea alpina*, *Parnassia palustris*, and *Melandryum apetalum*.

Myosotis sylvatica occurred in small quantity up to fully 50 feet beyond the extreme limit of *Betula odorata*.

At 3900 feet the undergrowth of the willows and dwarf birch was dominated by *Salix reticulata*, *Euphrasia officinalis* var. *Astragalus alpinus*, *Parnassia palustris*, *Polygonum viviparum*, *Trisetum subspicatum*, and *Carex atrata*.

On the Nystuhöerne or W. side of the valley the shrubs were not so dense, and at 3850 feet both *Lychnis alpina* and *Azalea procumbens* made their appearance. At the head of the valley *Lychnis alpina* occurs at a little over 3000 feet in the open lichen-formation.

Phaca frigida extends right through the shrubland and is much affected by a *Puccinia*.

Thalictrum alpinum also occurs in small quantity through this zone, and was frequently attacked by an *Æcidium*.

Nothing could be more conspicuous than the leaves of *Vaccinium uliginosum* and *V. Vitis-idæa* attacked by the parasite *Exobasidium Vaccinii*, the bright crimson leaves being quite a feature of the upper reaches of this zone.

The upper limit of the shrubland is not very well defined, but is approximately 4,500 feet, although *Betula nana* in straggling dwarfed individuals goes to 4,800 feet, and stunted specimens of *Salix lanata* were observed up to 4,900 feet. As the larger shrubs begin to thin out, *Salix reticulata* becomes very abundant, attaining its maximum development about 4,400 feet and extending up to 4,800 feet. *Salix herbacea* becomes dominant where the *S. reticulata* ceases, and reaches its maximum abundance about 4,700—4,800 feet, after which it rapidly diminishes in amount up to 5,000 feet. Where *Salix herbacea* is thus abundant it carpets the ground, forming a dense mat to the exclusion of most other plants.

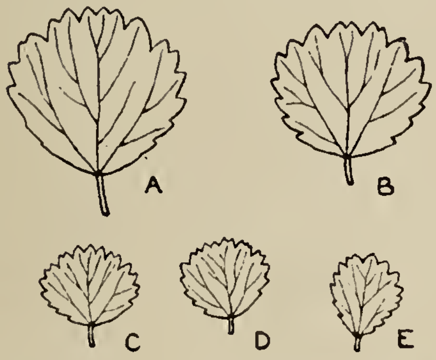

Fig. 27. A and B, leaves of *Betula nana* from an altitude of 3,200 feet; C–E, leaves from an altitude of 4,800 feet. Natural size.

Betula nana near its highest limit is much stunted and its leaves much reduced in size. Fig. 27 A—E shows the striking contrast in the size of the leaves of plants growing at 3,200 feet and those growing at or near the upper limit of 4,800 feet. There are also differences in anatomical structure which are due to this difference in altitude. The large leaves from the lower altitudes are somewhat thicker, with a palisade tissue of two and a portion of a third or often of three complete layers, whereas the palisade of the small leaves from high altitudes consists of one complete layer and a second smaller and more or less incomplete layer. The spongy mesophyll cells are also larger and more inflated (*vide* Fig. 28 A and B).

One character, possessed by all the leaves of *Betula nana* examined, irrespective of altitude, is the presence of an incomplete layer of hypodermal cells beneath the upper epidermis. This layer is derived from the upper epidermis, the cells of which are of variable size. Their outer walls are more or less plane, whereas their inner walls are very convex and quite commonly hemispherical. They are also of very variable depth. The majority of these cells are divided by a wall parallel to the surface of the leaf and nearer the outer than the inner wall.

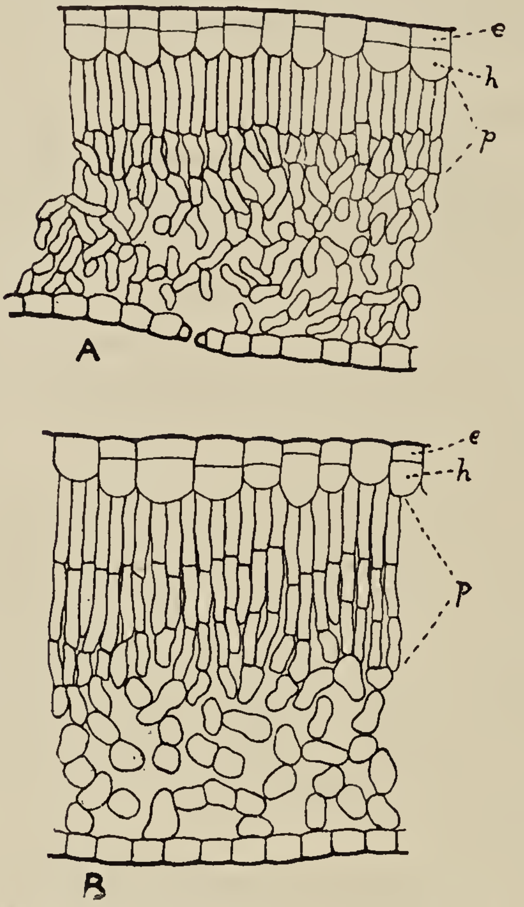

Fig. 28. A, section of leaf of *Betula nana* from 4,800 feet; B, section of leaf from 3,200 feet. *e*, epidermal cell; *h*, hypodermal cell; *p*, palisade cells.

Thus, a relatively large hypodermal cell has been cut off from a narrower epidermal cell. The dividing-wall and the other walls of the hypodermal cells are exceedingly thin, with a still thinner lining protoplasmic layer, the interior of the cell being occupied by a colourless cell-sap vacuole. The outer walls of the epidermal cells are fairly strong and well cutinized. Such a hypodermal layer does not appear to have been observed in species of *Betula*, although a number of species of *Alnus* possess a hypoderma.

The hypodermal cells of *Betula nana* are both conspicuous and irregular, the palisade cells extending upwards and filling up the irregularities. The walls are so delicate and the vacuoles so completely fill these cells, that we can only regard them as constituting a slight development of aqueous tissue. It should be remarked that *Betula nana* grows for the most part in very exposed situations, where it is subject to almost continuous winds.

On the flatter ground near the upper limit of shrubs were a number of boggy patches, those on the Nystuhöerne side of the valley being much the most extensive (*vide b*, *b*, on chart). There was almost an entire absence of *Sphagnum* from these bogs, and the part usually played by species of this genus in alpine bogs was here taken up by *Amblystegium sarmentosum*, which occurred in immense quantity. Other less abundant mosses were *Paludella squarrosa*, *Philonotis tomentella*, a form of *Dicranum Bonjeanii*, *Amblystegium fluitans*, *A. exannulatum*, *A. cordifolium*, *A. aduncum*, and *A. intermedium*. In the tiny streams slowly finding their way into bogs were dense cushions of the gregarious *Koenigia islandica*, occasionally associated with *Montia fontana* and *Epilobium alpinum*.

VIII.—ALPINE LICHEN-PASTURE.

[Marked L on the Chart.]

Above the somewhat indefinite limit of the shrubs one passes into the alpine pasture, which in a great measure consists of fruticose lichens: so much so, in fact, that the whole of this upland area is really an extensive *lichen-formation*. This great expanse of lichens exist not merely where the ground is rocky and precipitous, but also covers square miles of the more or less level upland areas. Walking over this lichen-formation gives rise to peculiar sensations, as the lichens are from three to five inches in depth. In wet weather it is a carpet of softness beyond conception; in the hot sunshine every step crushes a number of these upstanding lichens into fine powder. This lichen-formation constitutes the pastures of the reindeer, and consists chiefly of the following six lichens:—*Platysma nivale* (with *P. cucullatum* in small patches), *Cladonia sylvatica* var. *alpestris*, *Cl. rangiferina*, *Alectoria ochroleuca* (and small quantities of *A. rigida*), *Stereocaulon alpinum*, and *Cetraria islandica*. The first-mentioned was generally dominant, and the others locally so. The *Alectoria*, when dominant, was in the most exposed places. Other lichens occurred sparingly amongst those already mentioned, the chief of which were:—*Cetraria aculeata*, *Cladonia degenerans*, *Cl. furcata*, *Cl. cariosa*, *Cl. gracilis* (and its var. *macrocera*), *Cl. cervicornis*, and *Sphærophoron coralloides*.

Flowering plants are dotted amongst the lichens, either as individuals or in clusters, sometimes in widely open formation and at other times in much closer formation. *Lychnis alpina* often stands out conspicuously (*vide* Pl. 2, Fig. 2), and great cushions of *Silene acaulis* are common up to 4,750 feet. These large mat-like cushions of *Silene acaulis* are quite a feature of the open phanerogamic formation, and often reach a diameter of two feet. An examination of the leaf-structure, *shows the stomata to be exclusively confined* to *the upper surface*, a fact which is correlated with the dense character of the mats, only the upper surfaces of the leaves being freely exposed to the air.

Veronica alpina, blue both in the flowering and fruiting conditions, is frequent, and in the damper places near trickles of water the yellow flowers of *Draba alpina* are obvious even at a distance. *Pedicularis Œderi* does not extend above 4,700 feet, and *P. lapponica* scarcely enters this zone at all. *Arabis alpina* can be observed up to 5,100 feet, and stunted varieties of *Taraxacum officinale* extend along with *Carex rigida* to fully 5,000 feet. *Ranunculus nivalis* begins at 4,900 feet near the head of the valley, but further down near the "Vaarstien" it makes its appearance at just over 4,000 feet.

Ranunculus glacialis first appears at about 4,800 feet. No alpine plant has a more characteristic habitat, occurring as it does on the loose gray debris of ice-slides, snow-slides, and glaciers. On the mountains at the head of the Driva valley it occurs in suitable places in great quantity, and owing to its exposed situation is subject to a continuous wind-action.[1] Where this plant grows the ground contains much fine detritus and is always more or less saturated with water, and this fact probably accounts for the leaf-structure, in which the stomata are for the most part on the upper surface. The palisade is three layers in thickness, and under each stoma is a large respiratory chamber in the upper layer. The spongy mesophyll possesses extraordinarily large intercellular spaces.

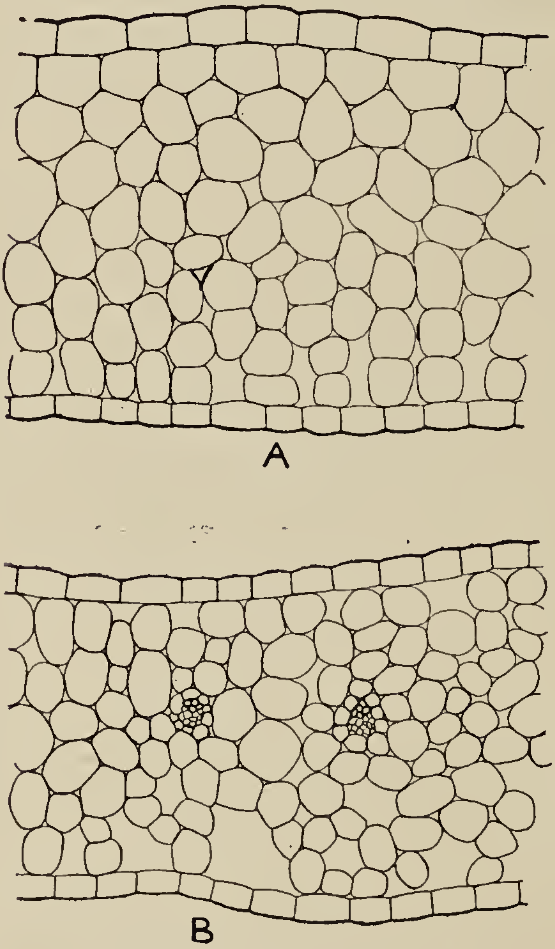

Fig. 29. Transverse sections of leaves of *Sedum Rhodiola* from an altitude of 4,900 feet. A, in very dry situation; B, from wet place. Sections under same magnification.

Special comment is necessary on the occurrence of *Sedum*

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[1] During four weeks in the month of August, with many fine sunny days, it was not possible owing to the wind to obtain a photograph of the magnificent clusters of flowers of *Ranunculus glacialis* which occurred so profusely at the higher altitudes.

Rhodiola. This plant is exceedingly abundant both in the valley and on the surrounding mountains, occurring in greatest quantity at about 4,900 feet. At the lower altitudes it grows well in its normal habitat in the cracks and fissures of rocks, but at the higher altitudes it occurs in a somewhat stunted form in the lichen-formation, and even among wet mosses at the sides of the small streams! Two plants were specially preserved for anatomical investigation, one from a constantly wet place, and another which was growing close by the first one, but on the dry summit of a rock. They showed marked differences in the structure of the leaves. That growing in the dry place had relatively thick leaves with large mesophyll cells and relatively few and small intercellular spaces. The cells of the upper epidermis were also considerably larger than those of the lower epidermis. The plant growing in the wet situation had thinner leaves and much smaller mesophyll cells. The intercellular spaces were numerous and often large, and both upper and lower epidermis were of a similar character (*vide* Fig. 29A and B).

In and about the trickles of water coming from melting snow between the two summits of Knutshö, and in one of the bleakest and most exposed situations on the whole mountain, were tufts of *Phippsia (Catabrosa) algida.* This inhospitable spot was about 5,000 feet and among some extensive snow slopes. The leaf of this grass is short and blunt, reaching a length of about an inch. It is a leaf characteristic of cold, exposed situations, and in transverse section is nearest to the leaf of *Aira præcox*[1]. It is a folded leaf, with two folds, and motor-cells at each fold, as in *Catabrosa aquatica.*

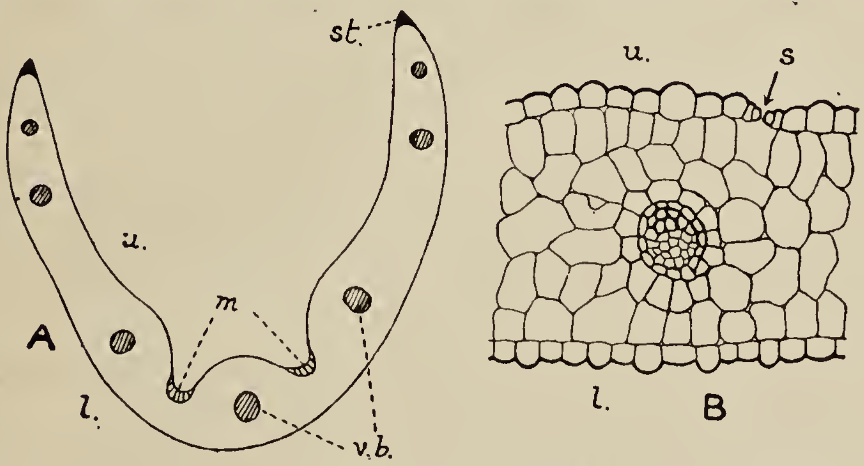

Fig. 30. Leaf of *Phippsia algida* (=*Catabrosa algida*). A, transverse section to show the folding of the leaf, the seven vascular bundles (*v.b.*), the position of the motor cells (*m*) and the very small amount of stereome (*st.*) B, part of transverse section of leaf to show the nature of the epidermis and the mesophyll. *u*, upper surface; *l*, lower surface.

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[1] L. Lewton-Brain, "Anat. Leaves Brit. Grasses," Trans. Linn. Soc. Bot., 2nd. ser., Bot. vi., 1904, t. 36, f. 5.

The cells of both upper and lower epidermis are greatly arched outwards and strongly cuticularized. Stereome is scarcely developed, being present only at the extreme edges of the leaf and in very small amount. There is none even at the mid-rib. There are seven vascular bundles, each one possessing a double sheath consisting of an outer layer of large cells and an inner layer of small cells. The bundles have no vessels and no intercellular spaces. There are only three ridges (seen as rounded elevations in transverse section) on the upper surface of the leaf corresponding to the three median bundles. The mid-rib projects on the upper surface only. The mesophyll is compact and continuous, with very minute intercellular spaces, and all the cells contain chloroplasts. The stomata are disposed in about six rows on the upper surface and a single row near each edge of the leaf on the lower surface. The xerophytic characters of this grass are due mostly to the coldness at its roots and partly to continuous cold winds.

The actual summit of Knutshö (5,602 feet) is a steep rocky mound of several hundred feet, the rock-surfaces being thickly and entirely covered with lichens. In the large holes of the great rocks was an abundance of the hepatic *Chandonanthus setiformis*, occurring in characteristic golden-green patches. Associated with it in some of the patches were *Jungermannia Lyoni*, *Dicranum molle* and *Hylocomium proliferum*. The lichen *Pilophorus robustus* occurred here in fine fruit. In many of the crevices individual and tufted flowering plants occur. The following species were noticed to the very summit:—*Saxifraga cæspitosa*, *Salix herbacea*, *Oxyria digyna*, *Polygonum viviparum* (without flowers), *Luzula arcuata*, *Poa stricta*, and *Aira flexuosa* var. *montana*.

On the west side or Nystuhöerne side of the valley the shrubland zone is not so dense, and as it passes into the alpine pasture there are a number of marshy and boggy places. *Sibbaldia procumbens* was abundant in the detritus brought down by the snow, and was often associated with *Gnaphalium supinum*, as is the case in many of the Perthshire mountains. *Eriophorum Scheuchzeri* and *Hieracium alpinum* were often conspicuous, and among the gravelly soil was an abundance of fruiting *Conostomum boreale*. Great masses of *Paludella squarrosa* occurred alongside sheets of *Hypnum sarmentosum* (in fruit), while on higher slopes of fine debris left by melting snow was an abundance of *Polytrichum sexangulare* among patches of *Ranunculus glacialis*. *Splachnum vasculosum* and *S. pedunculatum* were frequent on the old stercoral deposits of cattle, *Tetraplodon bryoides* on old remains of dead animals, and in some of wet places *Sphagnum rubellum* and *S. fuscum* formed small dense cushions, the older masses of which were sometimes covered with *Bæomyces icmadophilus.* On the rocks were *Parmelia lanata, Gyrophora polyrhiza, G. arctica, G. hyperborea* and *G. erosa.* One of these bogs contained quantities of *Carex rariflora.* Scattered through the lichen-formation of this side of the valley were numerous cushions of *Andromeda hypnoides* and *Cardamine bellidifolia.* Near the rills *Saxifraga rivularis* was frequent. A form of *Hypnum palustre* was frequent and in the wet glacial mud were dense patches of *Pohlia ludwigii,* with *Hypnum Heufleri, Desmatodon latifolius* and a form of *Rhacomitrium canescens* on the drier ground, the latter among sand. On wet rocks in the streams of melted snow, *Hypnum Goulardi* and *H. badium* were abundant.

8A,—THE PLATEAU AT THE HEAD OF THE VALLEY.

This agrees in general features with the alpine lichen-pasture, but although very bleak the altitude is not so great, and there are in consequence quantities of scattered shrubs of *Betula nana, Juniperus nana,* and the dwarf species of *Salix* (consult Pl. 2, Fig. 1).

Stems of *Betula nana* from this bleak area and also from near their upper limit on Knutshö were examined for their structure. The amount of wood annually added was by no means small, stems eight years of age having a diameter of 5·8 mm.

Stems of *Juniperus nana* from the same spots showed growth to be much slower. A stem 5·8 mm. in diameter was 30 years old. Four concentric series of tracheides was quite a usual number to be added in one growing season, and sometimes only two were added. The maximum number observed was eleven.

On the more exposed parts the carpet of lichens is very thick, and consists of the following species in varying proportions, sometimes one being dominant and sometimes another:–*Stereocaulon alpinum, Alectoria ochroleuca, A. rigida, Platysma nivale, P. cucullatum, Cladonia rangiferina, Cl. sylvatica,* and *Cl. furcata.* At the higher elevations *Platysma cucullatum* became more abundant and *P. nivale* less abundant. On the

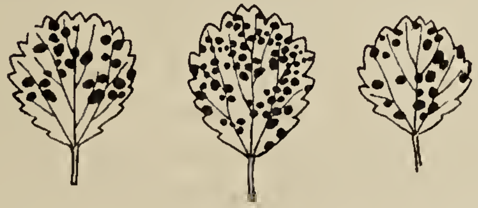

Fig. 31. Leaves of *Betula nana* attacked by a leaf-blotch fungus (*Rhytisma* sp.) Natural size,

sheltered side of the rocks, *Betula nana*, *Arctostaphylos Uva-ursi*, and *Empetrum nigrum* occurred in about equal proportions. In a few places *Arctostaphylos alpina* was very abundant.

A few of the more stunted specimens of *Betula nana* were attacked by a species of *Rhytisma*, and as no species of this genus has previously been observed on the leaves of the dwarf birch, it is probable that the fungus is as yet undescribed (Fig. 31).

In the more open places *Festuca rubra* and *Carex rigida* were everywhere present. Most specimens of the latter in this area were attacked by *Ustilago Caricis*, a fungus which so far as we can ascertain, has not previously been recorded as attacking *Carex rigida*. *Kobresia bipartita* was also a constituent of the turf in many places.

Among the lichens were patches of *Nephromium arcticum* and occasionally *Cladonia degenerans*. On the rocks were *Cetraria aculeata*, *Lecidea geographica*, *Lecanora tartarea* (scarce), *Parmelia saxatilis*, *Gyrophora proboscidea*, *G. hyperborea*, *G. cylindrica*, *G. arctica*, and *G. polyrhiza*.

Near the sides of the old road to Hjerkin, and in some of the more open spaces, were patches of dense turf consisting of *Poa alpina*, *Poa glauca*, *Festuca rubra*, *Trisetum subspicatum*, *Juncus trifidus* and *Carex incurva*. In this turf were numerous specimens of a species of *Russula*, very similar to, if not identical with, *Russula emetica*. The fruit-bodies showed a very striking adaptation to the exposed conditions under which they existed. The turf was very dense and the top of the pileus of the *Russula* never reached so high as the short grass-leaves amongst which the fructification was growing. Moreover, the edge of the pileus was invariably incurved in the manner shown in Fig. 32. This agaric thus presented a somewhat peculiar appearance, each individual looking like a large red button sunk in the dense mat of turf, which grew in such a compact manner around the pileus that the gills would never be exposed to the excessive wind.

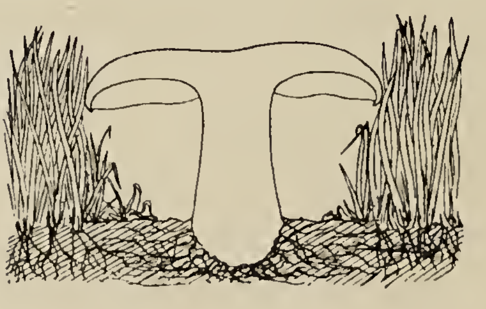

Fig. 32. Diagrammatic section to show the relation of the fruit-body of *Russula* sp. with the surrounding turf, in very exposed situations at about 3,200 feet.

Towards the Goveli lake, and round about the stream which issues from this sheet of water, was a boggy area [b^1, b^1 on the chart] with an abundance of *Amblystegium trifarium*, and *A.*

scorpioides. Some parts of this bog were occupied by *Carex vaginata*, *C. pulla*, *C. limosa*, and an alpine form of *C. Goodenoughii*, others by *C. dioica*, *C. polygamum*, *C. microglochin* and *C. capitata*, while *Eriophorum alpinum* was frequent in small patches. In the stream were quantities of *Carex aquatilis* var. *sphagnicola* and *Hippuris vulgaris*, and some of the small bog-pools contained the minute form of *Utricularia minor* previously mentioned as having been found near Hjerkin (consult Fig. 26).

It should be mentioned that although *Rubus Chamæmorus* abounds in most parts of Norway, it was a scarce plant in this part of the Dovrefjeld. Probably the climate is too cold and the edaphic conditions are not suitable except in very small areas. *Calluna vulgaris* is very rare, and *Erica cinerea* and *E. Tetralix* are entirely absent. *Andromeda polifolia* was not frequent, and *Vaccinium Oxycoccus* was decidedly uncommon.

The scarcity of Sphagna should again be emphasized, as they were very uncommon even in those places where one is accustomed to find them in great quantity in Britain, the boggy areas being occupied very largely by *Hypnum sarmentosum*, often associated with *Paludella squarrosa*. In one rather extensive marshy area tall specimens of *Catascopium nigritum* occurred in dense masses dominating the whole area.

Hepaticæ are by no means frequent in this district, probably owing to the lack of sufficient warmth and atmospheric humidity in the growing season, and to the length of the cold winter.

The rainfall is low, the average for the district, as kindly supplied to us, with other data, by Mr. Sigurd Holaker, the proprietor of the Kongsvold station, is about 350 mm. (13·77 inches).

The average temperature is 0·8°C. The average winter temperature is about—25°C. The snow lies on the ground from six to seven months. The latitude is 62° 22′N. The station at the bottom of the valley is at an elevation of 2983 feet, and the height of Knutshö (less than three miles distant on the map) is 5602 feet.

On this journey we were accompanied by Mr. and Mrs. Ewing of Glasgow, to both of whom we would express our grateful thanks, not only for their esteemed companionship, but for the valuable information they were able to give us concerning the flora of the district, which they had previously visited several times. This information greatly facilitated the accumulation of the necessary data for this paper, and made it possible to accomplish considerably more in the space of a month, than could have been done by our unaided efforts,

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DESCRIPTION OF PLATES III. & IV.

ILLUSTRATING THE MESSRS. WEST'S PAPER ON THE ECOLOGY OF THE UPPER DRIVA VALLEY IN THE DOVREFJELD.

PLATE III.

Fig. 1. The exposed rocks near the road (marked "R" in the chart).

Fig. 2. The alpine shrubland on Knutshö at 4,000 feet, consisting mostly of "grey willows," *Betula nana*, and *Juniperus nanus.*

Fig. 3. Sand-bank near the river Driva covered with *Phleum alpinum.*

PLATE IV.

Fig. 1. The lichen-formation at the head of the valley in which there is a considerable admixture of stunted shrubs of *Betula nana* and *Juniperus nanus.*

Fig. 2. *Lychnis alpina* in the lichen-formation.

Fig 3. The crustaceous lichens on a vertical rock face on one of the lower slopes of Knutshö. A single specimen of a sp. of *Gyrophora* is visible in the picture. Note that the entire rock surface is covered with the prolific growth of lichens.

THE STUDY OF PLANT DISEASES.

[The following notes on some phases in the present day investigation of plant diseases have been written in the hope that they may prove of interest to botanists who are not primarily concerned with mycological research.]

ALTHOUGH some work had been done by Berkeley and others on diseases of plants prior to 1865, the critical study of certain groups of fungi as disease-producing organisms may be said to date from De Bary's observation in that year of the penetration of a host plant by the germ tube of a fungus spore and the subsequent development of a mycelium within the tissues. The clear establishment of the parasitism of certain fungi by this and similar observations gave an immense impetus to the study of fungi as agents in the production of disease amongst the higher plants. When one recognises that there is scarcely a plant of economic importance which is not subject to one or more serious diseases caused either by fungi or more rarely by bacteria, the importance of the study of mycology becomes manifest. From Rust in Wheat to Mildew on Vines and from Scab in Potatoes to Canker of Larch trees the story is always one of severe economic loss. Furthermore, the tendency of modern times is ever towards a more and more intensive cultivation of the soil, with the result that disease becomes increasingly prevalent. As an indication of the extreme possibilities of a fungus epidemic one may mention the well-known case of the destruction of the coffee plantation industry in Ceylon, on account of the attacks of the Rust Fungus *Hemileia vastatrix.*

It was obvious that before any measures of control of plant diseases could be introduced, a knowledge of the life histories of the organisms responsible for the injuries was essential. Thanks to the labours of Brefeld, Hartig, Klebahn, Marshall Ward, Massee and many others, the main outlines of the life-history of most of the fungi which are the agents of disease are now well known. In many cases the fungus suspected of being the cause of injury has been isolated from diseased plants and has been grown in pure cultures from which healthy plants have been subsequently infected. Although in the case of obligate parasites like the Rust Fungi it is not possible to grow these organisms upon artificial media, yet the course of development of many of these fungi from spore stage to spore stage has been so carefully followed that the part they play in inducing diseased conditions is clearly known.

Many kinds of treatment have been tried in regard to the control of such plant diseases as are here under consideration. Sometimes it happens that at one stage in the life-history of a destructive fungus the organism can be easily destroyed, whereas at other stages it is much more difficult to control. The Cherry Leaf Scorch Disease is a case in point. Cherry leaves attacked by this disease do not fall in the autumn because the presence of the fungus at the base of the leaf-stalk prevents the formation of the absciss layer. The only means of re-infection the following season is by spores formed in the perithecia which develop in the retained foliage of the previous year. Thus if leaves still hanging on the tree in winter time are collected and burnt there can be no danger of re-infection. But the matter is not always thus easy. With American Gooseberry Mildew, the practice which has been found most effective in control is the pruning of affected shoots from the bushes during the resting season and the destruction, by burning, of the perithecia attached to these shoots. If, however, the process of pruning is delayed beyond a certain time, the perithecia fall to the ground from the shoots, and there is great danger the following season of re-infection from the soil.

In the case of the heterœcious Rust Fungi, the eradication of one of the hosts involved in the life-cycle has been advocated in some cases. In this connection the Law of the State of Massachusetts passed in 1755, forbidding the planting of Barberry bushes in the neighbourhood of wheat fields, may be recalled. But where such a fungus possesses a uredo stage, the work of Marshall Ward[1] has shown the possibility of this phase of the life-history surviving the winter and causing re-infection the following season without the intervention of the alternate host.

Another means of controlling certain fungous pests is by the action of fungicides. The practice of spraying dates from the discovery by Millardet in 1883 of the toxic effect of Bordeaux Mixture (Copper Sulphate and Lime in certain proportions) upon diseases of the Vine. Bordeaux Mixture has ever since been deservedly popular with growers. Many other spraying fluids such as Liver of Sulphur, Lime-Sulphur, Formalin, etc., have come into use and sometimes are to be preferred to Bordeaux Mixture. It is clear that spraying will be most effective where the fungus is superficial, as in the Mildews. Spraying, however, is only a palliative in many cases and sometimes fungicides have almost no effect.

A more promising line of advance lies in the introduction of varieties of cultivated plants which are immune to certain fungous pests. When one begins to consider the question of disease in any group of organisms one is struck at the outset by differences in the degree of susceptibility present in various individuals. In agricultural and horticultural practice, variations in this respect are clearly recognised. Thus some varieties of potatoes are known to be immune from the Black Scab or Wart Disease, and there are strains of Wheat which are not attacked by certain Rusts. It must be remembered, however, that cases are known in which a variety may be immune in one locality and susceptible in another, and there is some evidence that the same variety may be resistant at one period of the year and readily affected at another.[2]

Biffen[3] has recently shewn that immunity from Yellow Rust (*Puccinia glumarum*) of a certain variety of wheat (Einkorn) is a character which can be bred on Mendelian lines and in this way wheats have been produced by hybridisation which combine heavy cropping properties with the power of rust-resistance.

[1] Ann. Bot., 1905.

[2] Cf. Howard. "Journal of Agricultural Science," 1907, p. 279.

[3] Biffen. "Journal of Agricultural Science," 1907.

Practically nothing is yet known as to the factors which confer immunity from specific fungous diseases. In the variety of wheat known as "Einkorn," which is immune from Yellow Rust, Miss Marryat[1] has shown that immunity is brought about by the too virulent attack of the parasite in its early stages of development. Thus instead of the fungus establishing a kind of symbiotic relationship with the host, it kills the cells in the immediate neighbourhood, and in consequence its progress into other living tissues is effectively barred. But the factors in the struggle between host and parasite, *i.e.*, the parts played by toxins and anti-toxins, and the influences of chemotropism are still obscure. Potter[2], working on a bacterial disease of turnips, has established the interesting fact that the disease can be checked by treatment with a sterilised extract of a culture on which the bacteria have been living for some time. The explanation of this phenomenon is that the organism secretes some substance which, upon being accumulated beyond a certain concentration, is detrimental to its own activity.

One of the most interesting discoveries of recent times in regard to the fungi is that of the existence of the phenomenon known as "specialised parasitism" in certain groups. Eriksson[3] was the first to show that Yellow Rust on Wheat was not physiologically the same as Yellow Rust on Barley, although these fungi cannot be distinguished morphologically. Thus uredospores of this Rust derived from wheat will not infect Barley, and *vice versâ*. Eriksson has determined the existence of many such specialised forms amongst the Rust Fungi which affect cereals.

Marshall Ward[4] followed up this work by determining that there may be "bridging host species" within certain cycles of alliance. Thus he found that the Brown Rust of the Brome grasses present in host species "A" will not infect host species "C," but can infect another species "B" and subsequently pass from "B" to "C."

Salmon,[5] working on the Mildews, has ascertained that the phenomenon of specialised parasitism is present in this group also. The same phenomenon has been discovered in other groups, but *Botrytis* and others appear to be pleophagous.

[1] Miss Marryat. "Journal of Agricultural Science," 1907.

[2] Potter. "Journal of Agricultural Science," 1908, p. 102.

[3] Eriksson. Ann. des. Sci. Nat., Vol. XIV.

[4] Marshall Ward. Ann. Myc., Vol. I.

[5] Salmon. Ann. Myc., Vol. II.

Another field of research in which much work has recently been done is that of tracing other stages in the life-history of parasitic fungi which were originally classed as "Fungi Imperfecti." Many of these organisms are virulent agents of disease and it has been a matter of some importance to ascertain if any higher stage is present in the full cycle of development. Thus the common scab of Apple Trees, *Fusicladium dendriticum*, is now known to be the conidial stage of the ascomycetous fungus *Venturia pomi*. Similarly the fungus causing the brown rot of fruit and originally called *Monilia fractigena*, really belongs to the ascomycetous genus *Sclerotinia*.

Considerable attention has recently been paid to the study of bacterial diseases of plants. A few years ago it was customary to doubt the existence of such diseases, partly on account of the fact that the cell-sap of the higher plants, possessing as it generally does an acid reaction, was thought to be inhibitive to the action of these organisms. This view has had to be modified in recent years and nowadays several well known diseases of plants are known to be induced by specific bacteria. Burrill in 1878 was the first to establish the existence of a definite bacterial disease, for in that year he showed that the Blight of Pear trees was due to a species of bacterium.

Erwin F. Smith of the United States has determined the presence of distinct bacterial diseases of Potato, Cabbage, Cucumber, etc., and Potter,[1] in this country has identified a bacterial disease of Turnips. In the current number of Science Progress, Potter gives a useful summary of the general progress that has so far been made in the study of pathogenic bacteria affecting the higher plants.

It may be of use at this juncture to say a few words about books dealing with plant diseases. The older continental books by Frank,[2] Sorauer,[3] Tubeuf,[4] Prillieux,[5] and others are still the most comprehensive although they do not deal with some of the diseases which have come into prominence during the last few years. Of Tubeuf's book there is an excellent English translation by W. G. Smith.[6] In regard to the special diseases of trees R. Hartig's book

[1] Potter. Proc. Roy. Soc., 1900.

[2] Frank. "Die Krankheiten der Pflanzen." 2nd edition. Breslau, 1895.

[3] Sorauer. "Handbuch der Pflanzenkrankheiten," Berlin, 1886.

[4] Tubeuf. "Pflanzenkrankheiten durch Kryptogame Parasiten verursacht," Berlin, 1895.

[5] Prillieux. "Maladies des plantes agricoles," Paris, 1895.

[6] Tubeuf and Smith. "Diseases of Plants induced by Cryptogamic Parasites," London, 1897.

is indispensable; it is available in the form of an English translation.[1] For those who wish to read a more philosophical treatment of plant pathology Marshall Ward's book entitled "Disease in Plants" (London, 1901) can be recommended.

Massee's "Text Book of Plant Diseases" has long been a useful book on the subject for English students although it is not so full as some of the works mentioned above. This book, however, has now been superseded by the issue of a larger work, "Diseases of Cultivated Plants and Trees"[2] from the pen of the same writer. The introductory chapters of this book are devoted to a consideration of Epidemics, Dispersal of Spores, Fungicides and other subjects of practical interest. The succeeding chapters deal with the life-histories of the disease-producing organisms, and suggestions are made as to measures of control. An important feature of the work is the lists of references to original papers which are given immediately after the descriptions of the fungi.

Another recent book on the same subject is by Professor Duggar, an American mycologist. This book, called "Fungous Diseases of Plants"[3] has been issued in an extremely convenient form. The illustrations are remarkably good, and the subject matter is written in a clear, terse, style. Another welcome feature of this work is the attention paid in it to culture methods and to the means of performing infection experiments. Of course the book has been written from the standpoint of American plant diseases, so that some diseases of importance in this country are omitted. Fuller information on the subject of bacterial diseases of plants is given in it than in other books on plant pathology. In reference to literature on the subject of bacterial diseases of plants mention should be made of Erwin F. Smith's manual entitled "Bacteria in relation to Plant Diseases."[4] The first part of this work dealing with culture methods has alone appeared as yet, and plant pathologists will eagerly look forward to the second part which will deal in detail with specific bacterial diseases.

F.T.B.

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[1] Hartig, R. "Text-book of the Diseases of Trees." Revised and edited by H. Marshall Ward, London, 1894.

[2] Duckworth & Co., London, 1910.

[3] Ginn & Co., Boston, New York, Chicago and London, 1909.

[4] Carnegie Institution, Washington, 1905.

ALPINE PLANTS.

The Plants of Alpine Switzerland.

By E. A. Newell Arber. London, John Murray, 1910,
pp. XI and 355. Price 7s. 6d. net.

MR. ARBER has written a book which will be very useful to those visitors to Switzerland who, without actually being botanists, desire to know something more than the ordinary tourist ever acquires, or wishes to acquire, about the fascinating Alpine flora. The author distinguishes the different natural habitats within the Alpine zone, such as Alpine pastures, meadows, woods, rocks, etc., and then picks out some representative groups of species from each, the Crowfoots and their allies, the Anemones, the Gentians, the Androsaces and Soldanellas, and so on, and describes their structure and habit, calling particular attention to their natural history. He writes clearly and attractively, and with knowledge, and even professional botanists may find a good deal to interest them in his discussions. If there is a fault to be found it is that the author rides his teleological horse a little too hard at times, so that the hardened and sceptical reader begins to wonder whether all the "adaptations" really originated for the purpose suggested, and whether the plants might not perhaps in many cases get on quite well without them! But perhaps this is hypercriticism as applied to a book which is not primarily addressed to the man of science; the adaptational point of view will certainly serve best to interest the general reader, and deeper considerations may well appear to the author to be rather out of place in such a work.

The photographs of alpine plants in their natural habitats are of quite exceptional beauty and excellence, and apart from its other merits would lend the work a distinction of its own.

A.G.T.

R. Madley, Printer, 151, Whitfield Street, Fitzroy Square, W.